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MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. II. THE *SOLIDAGO BICOLOR-S. HISPIDA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

The *Solidago bicolor-S. hispida* complex in the broad sense includes six species in *Solidago* subsect. *Squarrosae*: *S. bicolor, S. erecta, S. hispida, S. porteri, S. roanensis,* and *S. sciaphila*. While generally rather similar, each species is distinguished by different sets of indument and leaf and floral traits. *Solidago bicolor* has whitish rays while the other five have yellow rays. *Solidago bicolor, S. erecta, S. hispida*, and *S. roanensis* are diploid while *S. sciaphila* is tetraploid and *S. porteri* is hexaploid. A series of multivariate morphometric analyses were performed to discover additional technical traits useful in separating species.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 14 species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017). Semple and Cook (2006) recognized 9 species with infraspecific taxa in several species, while Semple (2017 frequently updated) recognized 14 species: *S. bicolor* L., *S. erecta* Pursh, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. Semple et al. (2017) informally divided the subsection into three species complexes based on a multivariate analysis of all 14 species and analyzed the *S. speciosa* complex in more detail. The *S. bicolor/S. hispida* complex includes the white rayed *S. bicolor* (Figs. 1-2) and the yellow rayed *S. hispida* (Figs. 3-4), *S. roanensis* (Figs. 5-6), *S. sciaphila* (Figs. 7-8), and *S. erecta* (Figs. 9-10), which was also included peripherally in the *S. speciosa* complex by Semple et al. (2017). *Solidago bicolor, S. hispida, S. roanensis,* and *S. erecta* are known only at the diploid level (Beaudry & Chabot 1959; Beaudry 1963, 1969; Kapoor 1970, 1977; Morton 1981; Semple et al. 1981, 1984, 1993; Love & Love 1982a; Semple & Chmielewski 1987; Semple and Cook 2004; unpublished data). *Solidago sciaphila* is the only tetraploid in the complex (unpublished data). The five species are overall morphologically similar but differ in stem hair density and distribution and differ in subtle ways in floral traits in addition to the obvious ray color difference. The very rare *Solidago porteri* is also most likely part of the *S. bicolor-S. hispida* complex but is readily recognized by it combination of large heads and stems that are glabrous proximally and sparsely to moderately hispid-strigose distally (see figures in Semple and Estes 2014). *Solidago porteri* is known from one location in south-central Tennessee, one location in northern Alabama, and several locations in central Georgia and is the only hexaploid in subsect. *Squarrosae* (Semple & Estes 2014).

The five species of the *Solidago bicolor/S. hispida* complex occur in overlapping ranges in eastern Northern America. *Solidago bicolor* occupies sandy, gravelly and loamy soils in open mixed woods, and wood and road margins and occurs from Nova Scotia and eastern Ontario south to Georgia and Alabama (Fig. 11). *Solidago hispida* occupies sandy or gravelly soils in open disturbed areas, crevices in rock outcrops, roadsides, prairies, woodland margins, open jack pine woods, and openings in mixed woods and is the most widely distributed species in the complex and (Fig. 12). *Solidago roanensis* (Fig. 13) occupies sandy or loamy, frequently moist, soils along roadsides, and on open rocky banks and mountain slopes, mixed deciduous woods and margins, oak-hemlock woods,

Figure 1. Morphology of *Solidago bicolor*: *Semple & B. Semple 11510* (WAT), Queens Co., Nova Scotia.

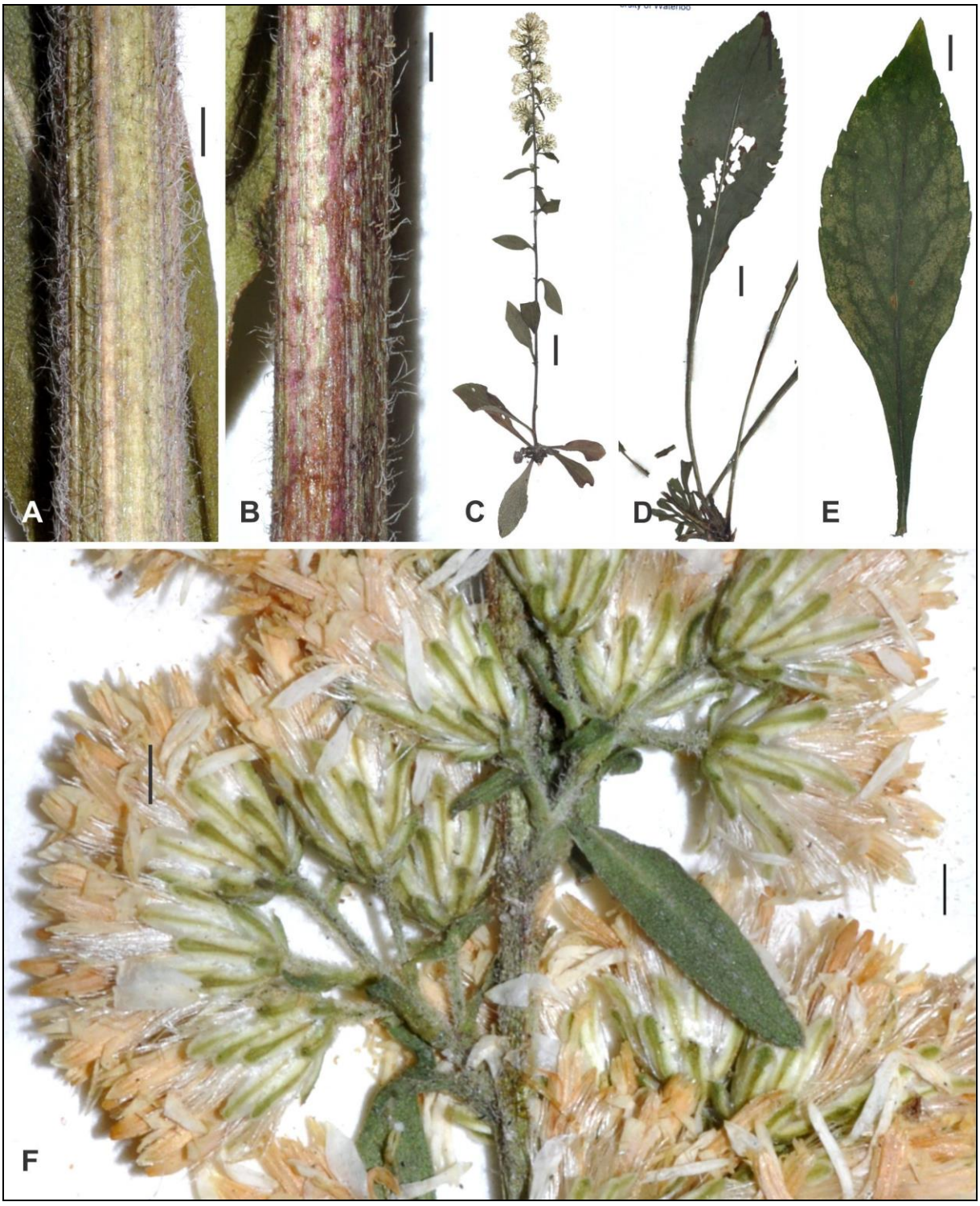

Figure 2. Details of *Solidago bicolor*. **A-B.** Mid stem hair density variation. **A.** *Semple & Keir 4592* (WAT), Québec. B. *Semple 3705* (WAT), Connecticut. C. Dwarf shoot, *Shchepanek & Dugal 3788* (WAT), Prince Edward Island. **D.** Basal rosette leaf, *Semple 10732* (WAT), Virginia. **E.** Lower stem leaf, *Semple & Suripto 9839* (WAT), Georgia. **F.** Heads with white rays, *Semple 3705* (WAT). Scale bars = 1 mm in A-B, F; = 1 cm in C-E.

Figure 3. Morphology of *Solidago hispida*: *Semple & Brammall 2846* (WAT, Sudbury Dist., Ontario.

Figure 4. Details of *Solidago hispida*. **A-F.** Mid stem hair length and density variation. **A-E.** Var. *hispida*. **A.** *Hamel C68020* (MT), "var. *lanata*" with long dense woolly hairs), Québec. **B.** *Semple & Brammall 2846* (WAT), Ontario. **C.** *Arnett & Hastings 1081* (LSU), Louisiana. **D.** *Doucet Do-59-6-15* (MT), Québec. **E.** *Baldwin 11518* (WAT), short dense canescent hairs, Saskatchewan. **F.** Var. *huronensis*, glabrous stem; *Morton & Venn NA7682* (WAT), Ontario. **G.** Var. *tonsa*, very small plant; *Morton & Venn NA12186* (TRT), Newfoundland. **H.** Var. *hispid*a, heads with yellow rays, *Fernald 12165* (MT), Québec. Scale bars = 1 mm in A-F and H; = 1 cm in G.

Figure 5. Morphology of *Solidago roanensis*: *Biltmore Herbarium 4622* (NY), Buncombe Co., North Carolina.

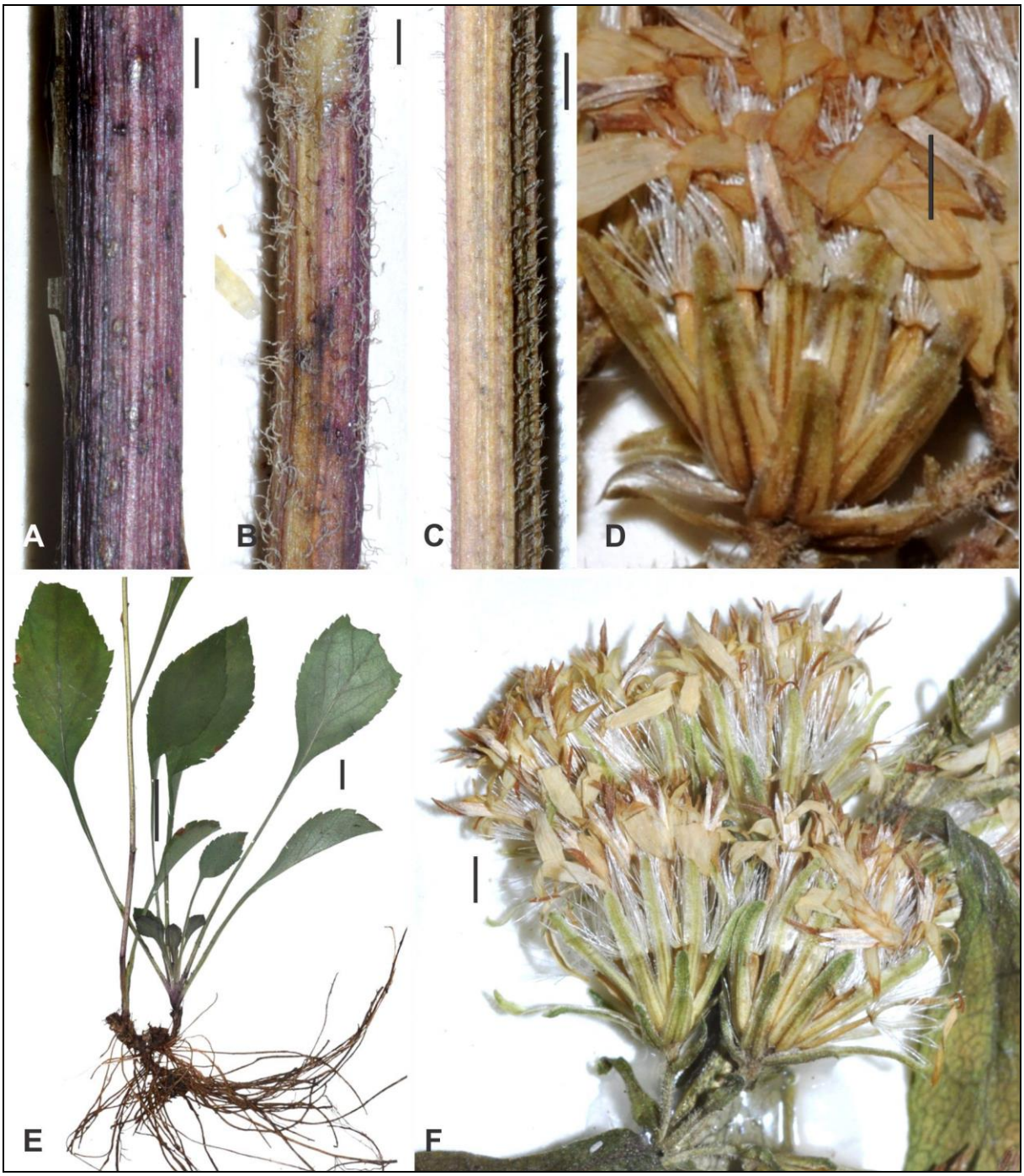

Figure 6. Details of **Solidago roanensis**. **A-B.** Lower and mid stems, *Radford 6481* (NCU), North Carolina. C. Mid stem, *Cannon 213* (NY), North Carolina. **D.** Multiveined phyllaries, *Cannon 213* (NY). **E.** Basal rosette, *Cusick 26911* (NY), West Virginia. **F.** Heads with yellow rays, *Poindexter 05-1937* (WAT), North Carolina. Scale bars = 1 mm in A-D, F; = 1 cm in E.

Figure 7. Morphology of *Solidago sciaphila*: *Zager 921005-6* (MIN), Houston Co., Minnesota.

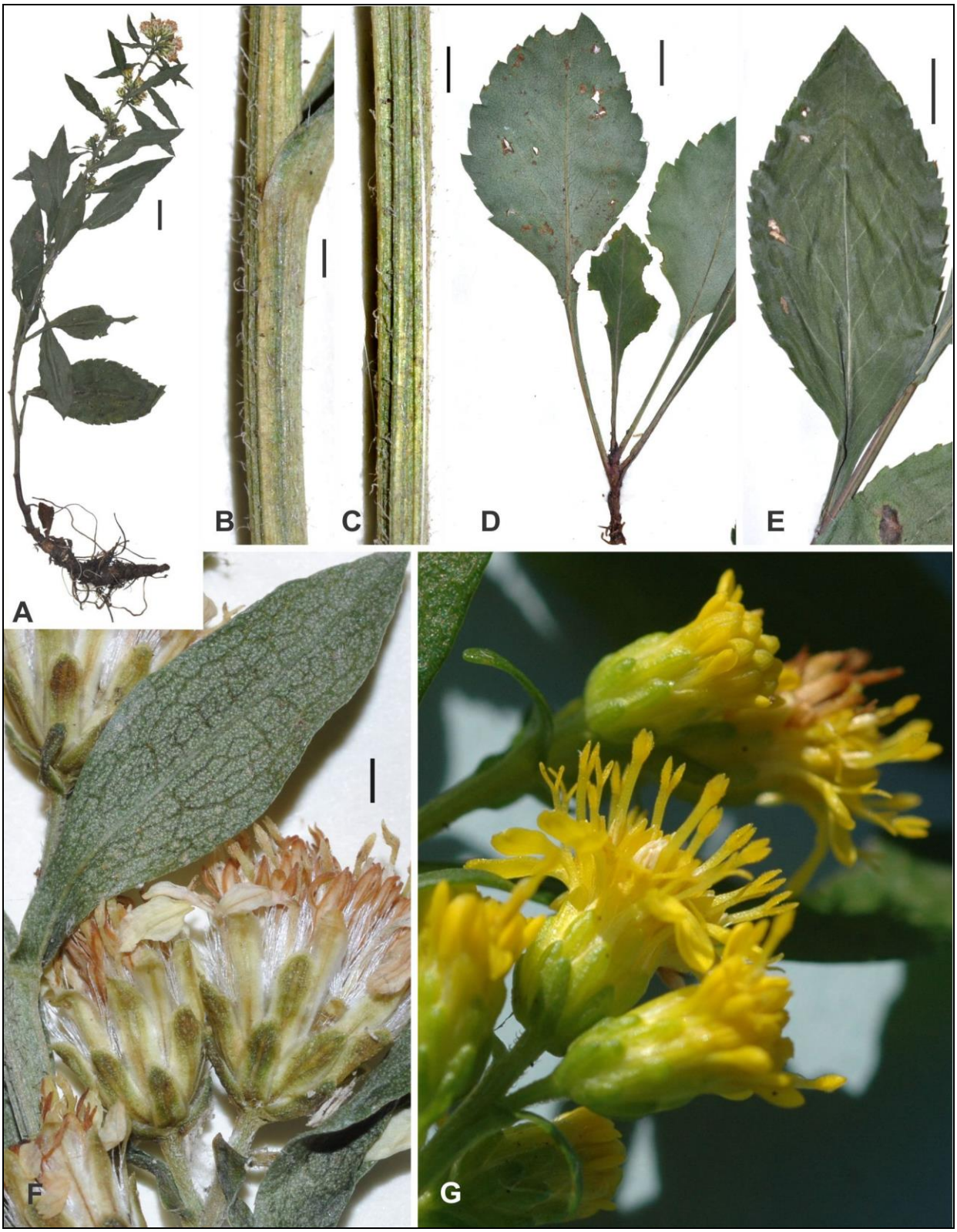

Figure 8. Details of the morphology of *Solidago sciaphila*. **A-D**. *Semple 11854* (WAT), Illinois. **A.** Small shoot. **B-C.** Lower and mid stem. **D**. Basal rosette leaves. **F-G**. *Semple 11851* (WAT),Wisconsin. **F.** Heads and bract, dried herbarium sheet. **G.** Heads, fresh in field. Scale bars = 1 mm in B-C, F; = 1 cm in A, D-E.

Figure 9. Morphology of *Solidago erecta*: *Semple 10771* (WAT) Sullivan Co., Tennessee.

Figure 10. Details of the morphology of *Solidago erecta*: *Semple 10771* (WAT), Sullivan Co., Tennessee. **A.** Lower stem. **B.** Mid stem. **C.** Stem in inflorescence, peduncles and head. **D.** Heads, rays yellow when fresh. Scale bars = 1 mm.

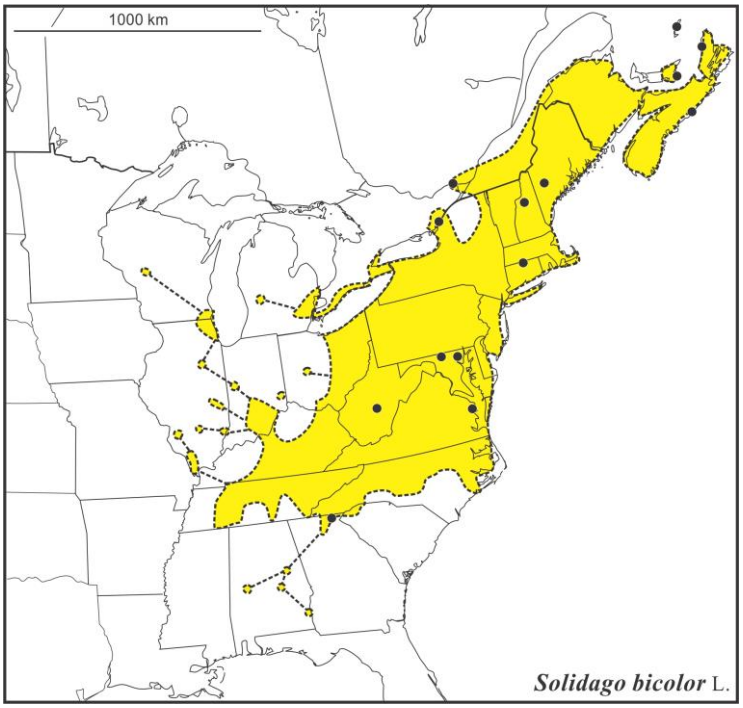

Figure 11. Range of distribution of *Solidago bicolor* and locations of specimens included in the analyses.

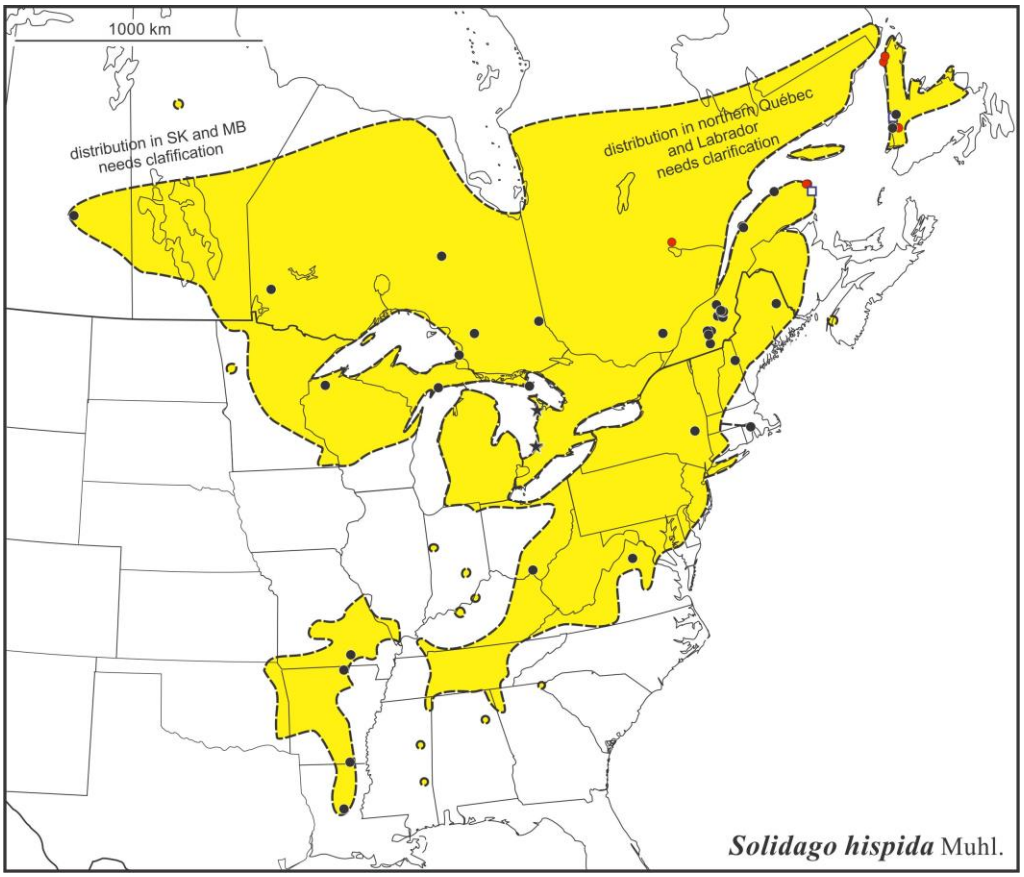

Figure 12. Range of distribution of *Solidago hispida* and locations of specimens included in the analyses: *var. arnoglossa* (red dots), var. *hispida* (black dots), var. *huronensis* (black stars), and *var. tonsa* (white squares).

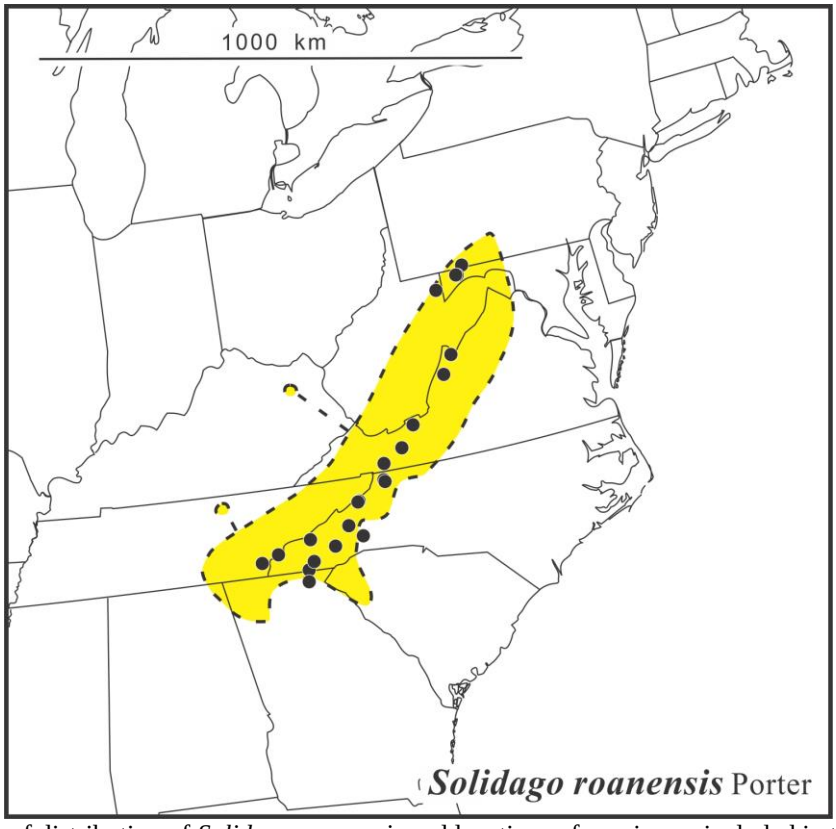

Figure 13. Range of distribution of *Solidago roanensis* and locations of specimens included in the analyses.

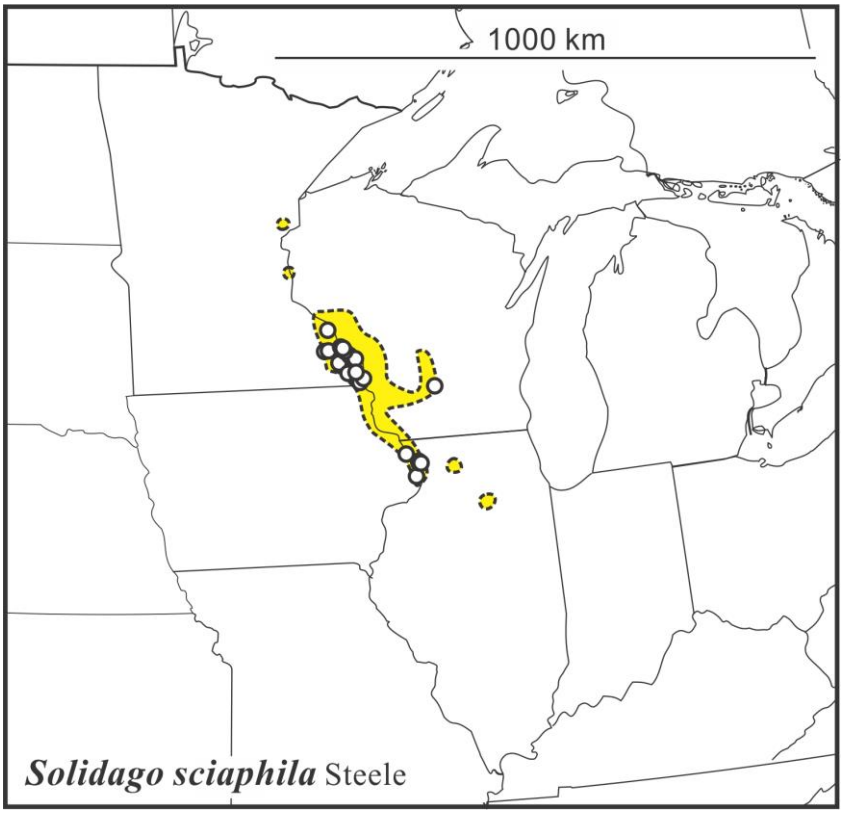

Figure 14. Range of distribution of *Solidago sciaphila* and locations of specimens included in the analyses.

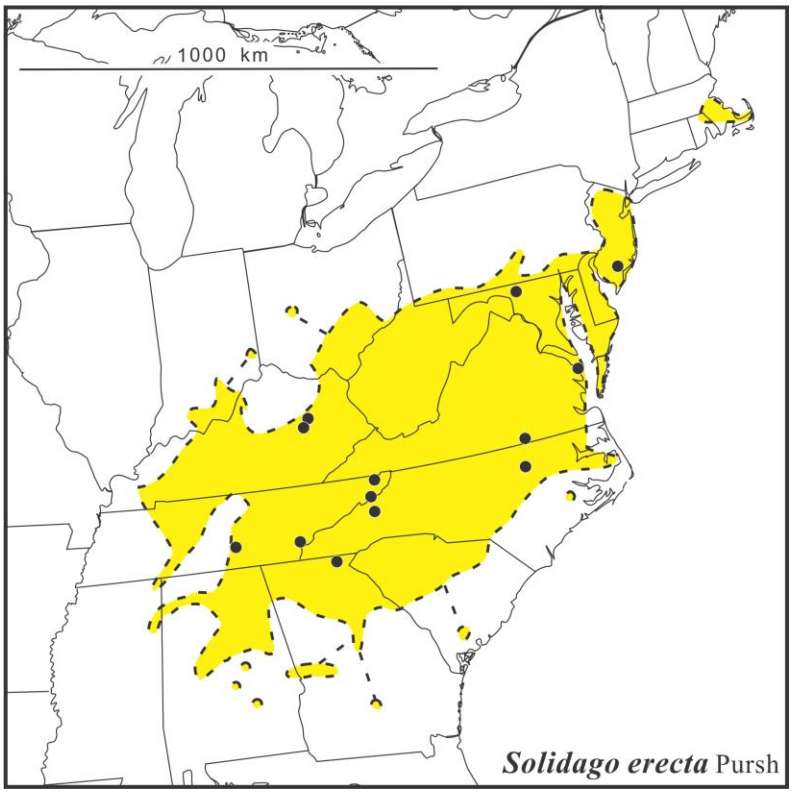

Figure 15. Range of distribution of *Solidago erecta* and locations of specimens included in the analyses.

and it occurs in the Appalachian Mountains from Pennsylvania to northern Georgia and Alabama. *Solidago sciaphila* occupies moist to dry rocky limestone and sandstone bluffs, dry dolomite cliff faces, in mixed pine and deciduous woods and margins, and is confined to much of the Driftless Area or Paleozoic Plateau of southwestern Wisconsin and adjacent states making it the only upper Midwestern species in the complex (Fig. 14). *Solidago erecta* occupies sandy clay and sandy loamy soils in open woods, along roadsides and road embankments, steep woody slopes, wet mixed hardwoods, cedar glades, and open pine woodlands on granite, and occurs at low to high elevations from Massachusetts to Georgia and northern Mississippi (Fig. 15) being generally more inland further south.

Solidago hispida is the most morphologically variable species in the complex and historically has been divided into eight varieties by multiple authors primarily on differences in stem and leaf indument: var. *arnoglossa* Fern., var. *disjuncta* Fern., var. *hispida*, var. *huronensis* Semple, var. *lanata* (Hook.) Fern, var. *luteola* Farwell, var. *ovalis* Farwell, and var. *tonsa* Fern. *Solidago hispida* itself has been treated as a variety within *S. bicolor*: *S. bicolor* L. var. *concolor* Torrey & A. Gray, *S. bicolor* var. *hispida* (Muhl.) B.S.P. Var. *arnoglossa* and var. *tonsa* were described from small to mid-sized less-hairy plants from Newfoundland (Fig. 4G). Var. *huronensis* was described from glabrous/ glabrate stemmed plants (Fig. 4F) native to sand dunes along the eastern shore of Lake Huron in Ontario; Fernald (1950) had included these plants in his var. *tonsa*. These three varieties appear to represent ecotypes adapted to local conditions within limited portions of the range of the species. Var. *lanata* was described from the western limits of the range in Saskatchewan (*Drummond s.n.*, GH ex Herb. Benth.!) and has the most densely woolly indument on stems occurring in the species. Fernald (1950) recognized var. *lanata* as occurring from Newfoundland to Saskatchewan across Canada. Densely woolly specimens collected in Ontario and Québec (Fig 4A) were included in this study. Stem hair density grades down to sparsely hispid-woolly stems (Figs. 4B-D). Sometimes the stem hairs are very short and the stems are canescent (Fig. 4E). With no obvious discontinuities in

stem hair density and length, most of these various indument forms have been lumped into var. *hispida* (Semple & Cook 2006). Included in the large sample of *S. hispida* in this study were specimens representing var. *arnoglossa*, var. *hispida* (including var. *lanata*), var. *huronensis*, and var. *tonsa*. Semple and Cook (2006) concluded that "other varietal names are based on minor variations".

No multivariate study of *Solidago hispida* or the entire *S. bicolor/S. hispida* complex has been previously published. The purpose of the study presented here is to compare and contrast morphological differences among the six species included in the complex using statistical methods.

MATERIALS AND METHODS

In total, 261 specimens from BALT, BOON, GA, LSU, MO, the J.K. Morton personal herbarium now deposited in TRT, MIN, MT, NCU, NEBC, NY, TAWES, UNB, and WAT in MT (Thiers, continuously updated) were scored and included in the analyses: *Solidago bicolor* (17 specimens), *S. erecta* (19 specimens), *S. hispida* (76 specimens representing four putative varieties), *S. porteri* (11 specimens), *S. roanensis* (20 specimens), *S. sciaphila* (20 specimens), and *S. speciosa* (23 specimens included in Semple et al. 2017). These were selected from more than 1700 specimens of *S.* subsect. *Squarrosae* examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016) and are not repeated here. Eight analyses were performed. In the first analysis, *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila* were included in STEPWISE discriminant analysis. In the second analysis, *S. bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* were included in a STEPWISE discriminant analysis. In the third analysis, *S. bicolor*, *S. roanensis*, and *S. sciaphila* were included in a STEPWISE discriminant analysis. In the fourth analysis, *S. bicolor*, *S. hispida*, *S. roanensis* were included in a STEPWISE discriminant analysis. In the fifth analysis, *S. hispida*, *S. sciaphila*, and *S. speciosa* were included in a STEPWISE discriminant analysis. In the sixth analysis, just *S. bicolor* and *S. hispida* were included in a STEPWISE discriminant analysis. In the seventh and eighth analyses on *S. hispida*, var. *arnoglossa*, var. *hispida*, var. *huronensis* and var. *tonsa* were included in STEPWISE discriminant analyses with different sets of characteristics.

Table 1. Traits scored for the multivariate analyses of 261 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf

MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RLAMLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RLAMPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

RESULTS

The Pearson correlation matrix yielded $r > |0.7|$ for most pairs of leaf traits reducing the number to be used to either mid leaf length, mid leaf width, or mid leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, petiole length, and length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Ray floret pappus body length at anthesis correlated highly with disc floret pappus length and only the latter trait was included in discriminant analysis of *Solidago bicolor*, *S. roanensis* and *S. sciaphila*, but these traits did not correlate as highly in the other combinations of taxa and were included in the analyses. Inflorescence length and width traits were highly variable in all species and were not included in the analyses.

Six species a priori groups analysis

In the STEPWISE discriminant analysis of 161 specimens of six species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila*), the following ten traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: number of ray florets (15.12), ray floret pappus length at anthesis (13.13), disc corolla lobe length (11.69), ray floret lamina length (7.50), number of disc florets (6.80), disc floret pappus length at anthesis (6.28), mid stem leaf width (6.10), inner phyllary length (5.90), outer phyllary length (5.81), and upper leaf margin serrations (3.99). Wilks's lambda, Pillai's trace, and Lawley-Hotelling

trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *S. porteri* and *S. hispida* (33.750), *S. porteri* and *S. roanensis* (31.233), and *S. porteri* and *S. sciaphila* (30.292), and the least separations were between *S. roanensis* and *S. sciaphila* (3.282) and *S. bicolor* and *S. hispida* (3.738).

In the Classificatory Discriminant Analysis of the six species level a priori groups (*Solidago bicolor, S. erecta, S. hispida, S. porteri, S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 63-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. All 11 specimens of the *S. porteri* a priori group (100%) were assigned a posteriori into the *S. porteri* group; 10 specimens with 100% probability, and 1 specimen with 96% probability. Fifteen of the 18 specimens of the *S. erecta* a priori group (83%) were assigned a posteriori to the *S. erecta* group; 13 specimens with 94-100% probability, and 1 specimen with 89% probability, and 1 with 69% probability (25% to *S. hispida*). Three specimens of the *S. erecta* a priori group were assigned to other species: 1 specimen to *S. sciaphila* with 94% probability (*Semple & Suripto 9688* WAT from Mt. Mitchell, North Carolina); 1 specimen to *S. hispida* with 54% probability (18% to *S. sciaphila*, 15% to *S. roanensis*, and 12% to *S. bicolor*; *Semple & Ringius 7659* WAT from Washington Co., Maryland); and 1 specimen to *S. hispida* with 37% probability (36% to *S. sciaphila*, 21% to *S. erecta*, and 5% to *S. roanensis*; *Kral 37937* WAT from St. Clair Co., Alabama; in the *S. erecta-S. rigidiuscula-S. speciosa* analysis in Semple et al. 2017 this was placed into *S. erecta* with 50% probability and into *S. rigidiuscula* with 49% probability). Thirteen of 17 specimens of *S. bicolor* (76%) were assigned a posteriori to the *S. bicolor* group: 4 specimens with 90-98% probability, 3 specimens with 83-88% probability, 4 specimens with 70-78% probability, and 2 specimens with 49% probability (49% to *S. hispida*; *Oldham 22125* WAT from the Magdalene Is., Québec) and 46% probability (41% *S. hispida* and 6% each to *S. erecta* and *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Four specimens of the *S. bicolor* a priori group were assigned a posteriori to three other species groups: 2 specimens to *S. hispida*, 1 specimen with 72% probability (22% to *S bicolor* and 4% to *S. sciaphila*; *Semple 10676* WAT from Greene Co., Pennsylvania) and 1 specimen with 45% probability (32% to *S. sciaphila* and 19% to *S. bicolor*; *Semple & Suripto 9839* WAT from Towns Co., Georgia); 1 specimen to *S. roanensis* with 62% probability (19% to *S. sciaphila* and 16% to *S. hispida*; *Semple 10656* WAT from Leeds Co., Ontario); and 1 specimen to *S. erecta* with 57% probability (27% to *S. bicolor* and 15% to *S. hispida*; *Semple 10732* WAT from Alleghany Co., Virginia). Fifteen of the 20 specimens of the *S. sciaphila* a priori group (75%) were assigned a posteriori to the *S. sciaphila* group: 3 specimens with 94-95% probability, 4 specimens with 85-89% probability, 1 specimen with 76% probability, 4 specimens with 66-68% probability, 2 specimens with 56% probability (28% to *S. hispida* and 14% to *S. roanensis*; *Dunevitz 911* MIN from Winona Co., Minnesota) and 55% probability (39% to *S. hispida*; *Dunevitz 1065* MIN from Wabash Co., Minnesota), and 1 specimen with 49% (*Zager 930907-5* MIN from Houston Co., Minnesota). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to other species groups: 4 specimens to *S. roanensis* with 85% probability (14% to *S. sciaphila*; Smith *14946* MIN from Houston Co., Minnesota), 59% probability (38% to *S. sciaphila*; *Tenney 545* MIN from Winona Co., Minnesota), 50% probability (48% to *S. sciaphila*; *Dunevitz 637* MIN from Winona Co., Minnesota), and 1 specimen with 38% probability (36% to *S. sciaphila* and 25% to *S. hispida*; *Dunevitz 693* MIN from Winona Co., Minnesota); and 1 specimen to *S. erecta* with 75% probability (14% to *S. hispida* and 8% to *S. sciaphila*; *Dunevitz 978* MIN from Winona Co., Minnesota). Twelve of 19 specimens of the *S. roanensis* a priori group (63%) were assigned a posteriori to the *S. roanensis* group: 8 specimens with 92-99% probability, 1 specimen with 71% probability, 2 specimens with 67% and 63% probabilities, and 1 specimen with 54% probability (46%

to *S. sciaphila*; *Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina). Seven specimens of the *S. roanensis* a priori group were assigned to two other species: 4 specimens to *S. sciaphila* with 88% probability (10% to *S. roanensis*; *Poindexter 05-1580* BOON from Ashe Co., North Carolina), 81% probability (10% to *S. roanensis* and 7% to *S. hispida*; *Williams s.n.* NY from Clay Co., North Carolina), 78% probability (22% to *S. roanensis*; *Cannon 213* NY from Avery Co., North Carolina), and 75% probability (*Biltmore Herb. 4622* NY from Buncombe Co., North Carolina); 3 specimens were assigned to *S. hispida* with 82% probability (6% each to *S. bicolor* and *S.* sciaphila and 5% to *S. roanensis*; *Radford 6481* NCU from Macon Co., North Carolina; phyllaries 1-veined), 65% probability (22% to *S. roanensis* and 13% to *S. bicolor*; *Boone s.n.4* TAWES from Garrett Co., Maryland), and 45% probability (36% to *S. roanensis* and 16% to *S. bicolor*; *Rydberg 8064* NY from Smyth Co., Virginia; phyllaries 1-veined); all 7 specimens had glabrous-glabrate lower stems, moderately to moderately dense hispid-strigose upper stems; and 5 of the 7 had multi-veined phyllaries. Forty-eight of 76 specimens of the *S. hispida* a priori group (63%) were assigned a posteriori to the *S. hispida* group: 4 specimens with 90-93% probability, 9 specimens with 81-87% probability, 16 specimens with 71-78% probability, 6 specimens with 60-68% probability, and 9 specimens with 50-59% probability. Twenty-eight specimens of the *S. hispida* a priori group were assigned to other species: 13 specimens were assigned to *S. bicolor* with 95-49% probability; 7 specimens were assigned to *S. sciaphila* with 95-49% probability; 5 specimens were assigned to *S. roanensis* with 81-41% probability, and 3 specimens were assigned to *S. erecta* with 88%, 67% and 61% probabilities.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 161 specimens of *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, S. *roanensis*, and *S. sciaphila* are presented in Fig. 16. Eigenvalues on the first three axes were 2.909, 0.920 and 0.56.

Table 2. Between groups F-matrix for the three a priori group analysis (df = 10 146).

Group	*bicolor*	*erecta*	*hispida*	*porteri*	*roanensis*
erecta	8.498				
hispida	3.738	13.173			
porteri	21.007	14.952	33.750		
roanensis	7.774	14.887	8.819	31.233	
sciaphila	10.762	13.195	8.637	30.292	3.282

Wilks' lambda = 0.0603 df = 10 5 155; Approx. F= 11.3889 df = 50 669 prob = 0.0000

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*erecta*	*hispida*	*porteri*	*roanensis*	*sciaphila*	% correct
bicolor	13	1	2	0	1	0	76
erecta	0	15	2	0	0	1	83
hispida	13	3	48	0	5	7	63
porteri	0	0	0	11	0	0	100
roanensis	0	0	3	0	12	4	63
sciaphila	0	1	0	0	4	15	75
Totals	26	20	55	11	22	27	71

Jackknifed classification matrix

Group	*bicolor*	*erecta*	*hispida*	*porteri*	*roanensis*	*sciaphila*	% correct
bicolor	9	1	6	0	1	0	53
erecta	0	15	1	0	0	2	83
hispida	15	3	46	0	5	7	61
porteri	0	1	0	10	0	0	91
roanensis	0	0	3	0	11	5	58
sciaphila	0	1	2	0	5	12	60
Totals	24	21	58	10	22	26	64

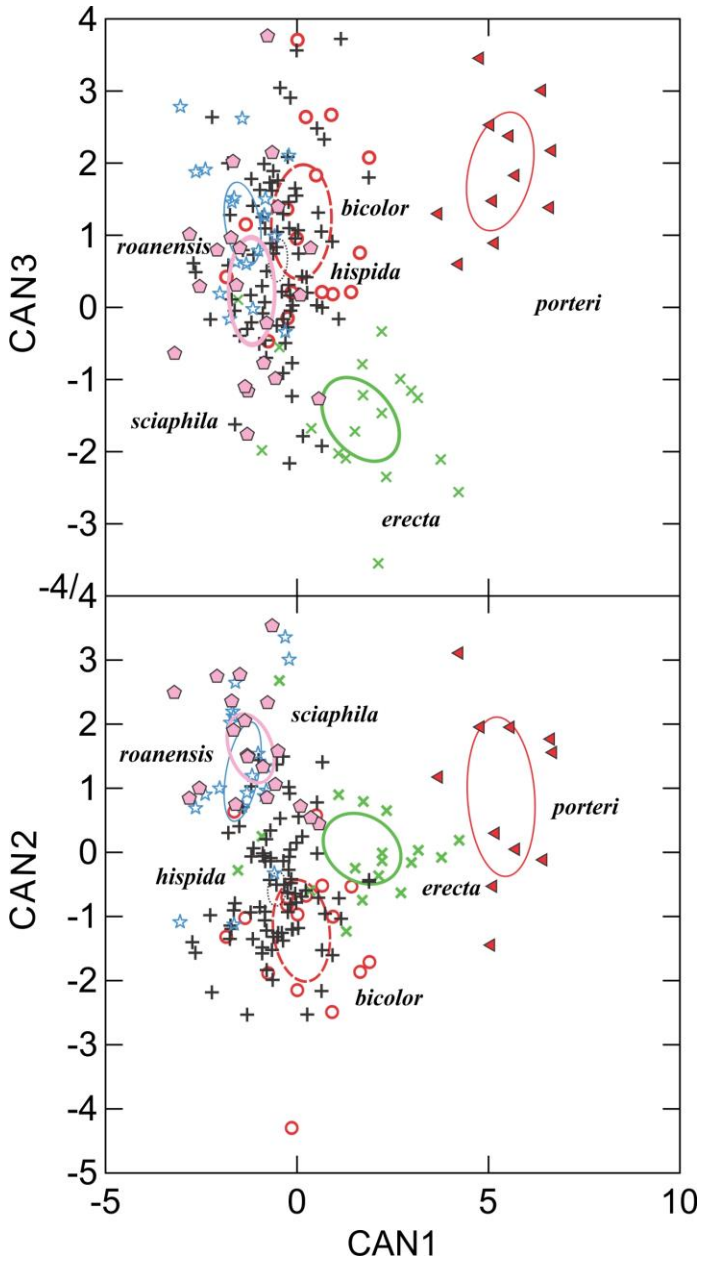

Figure 16. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 161 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. porteri* (red triangles), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Five species a priori groups analysis

In the STEPWISE discriminant analysis of 150 specimens of five species level a priori groups (*Solidago bicolor, S. erecta, S. hispida, S. roanensis*, and *S. sciaphila*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (25.94), number of ray florets (16.50), ray floret lamina length (10.19), mid stem leaf width (6.38), outer phyllary length (6.08), and inner phyllary length (5.43). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. erecta* and *S. roanensis* (20.807), and the least separations were between *S. roanensis* and *S. sciaphila* (3.110) and *S. bicolor* and *S. hispida* (5.328).

Table 4. Between groups F-matrix for the five a priori groups analysis (df = 6 140).

Group	*bicolor*	*erecta*	*hispida*	*roanensis*
erecta	13.253			
hispida	5.328	18.603		
roanensis	12.702	20.807	12.968	
sciaphila	15.668	17.751	13.062	3.110

Wilks' lambda = 0.1992 df = 6 4 145; Approx. F= 11.9813 df = 24 489 prob = 0.0000

In the Classificatory Discriminant Analysis of 150 specimens of the five species level a priori groups (*Solidago bicolor, S. erecta, S. hispida, S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 55-83%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. Fifteen of 18 specimens of the *S. erecta* a priori group (83%) were assigned a posteriori into the *S. erecta* group; 12 specimens with 90-100% probability, 1 specimen with 84% probability, and 2 specimens with 67% and 61% probabilities. Three specimens of the *S. erecta* a priori group were assigned to other species: 1 specimen to *S. sciaphila* with 84% probability (14% to *S. roanensis*; Semple *& Surpito 9688* WAT from Mt. Mitchell, North Carolina; lower and mid stems are glabrous); and 2 specimens to *S. hispida* with 43% probability (26% to *S. erecta* and 18% to *S. sciaphila*; *Kral 37937* WAT from St. Clair Co., Alabama) and 41% probability (29% to *S. bicolor*, 24% to *S. roanensis*, and 6% to *S. sciaphila*; *Semple & Ringius 7659* WAT from Washington Co., Maryland). Thirteen of the 17 specimens of the *S. bicolor* a priori group (76%) were assigned a posteriori to the *S. bicolor* group; 3 specimens with 92-93% probability, 6 specimens with 82-88% probability, 2 specimens with 76% and 61% probabilities, and 2 specimens with 63% and 60% probabilities. Four specimens of the *S. bicolor* a priori group were assigned to other species: 1 specimen to *S. erecta* with 77% probability (17% to *S. hispida* and 5% to *S. bicolor*; *Semple 10732* WAT from Alleghany Co., Virginia), 1 specimen to *S. roanensis* with 61% probability (25% to *S. sciaphila and 122% to S. hispida*; *Semple 10656* WAT from Leeds Co., Ontario), 1 specimen to *S. hispida* with 57% probability (39% to *S. bicolor*; *Semple 10676* WAT from Greene Co., Pennsylvania), and 1 specimen to *S. sciaphila* with 44% probability (24% to *S. hispida*, 20% to *S. bicolor* and 11% to *S. roanensis*; *Semple & Suripto 9839* WAT from Towns Co., Georgia). Fifteen of

the 20 specimens of the *S. sciaphila* a priori group (75%) were assigned a posteriori to the *S. sciaphila* group: 3 specimens with 87% probability, 3 specimens with 73-76% probability, 4 specimen with 60-67% probability, 3 specimens with 57% probability (30% to *S. roanensis*; *Shinners 4706* MIN from Columbia Co., Wisconsin), 54% probability (36% to *S. hispida*; Zager 930907-5 MIN from Houston Co., Minnesota), and 54% probability (23% to *S. roanensis* and 11% to *S. erecta*; *Shinners S-44-627* MIN from Carroll Co., Illinois). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to the other groups: 1 specimen to *S. erecta* with 64% (19% to *S. hispida* and 10% to *S. sciaphila*, and 6% to *S. bicolor*; *Dunevitz 978* MIN from Winona Co., Minnesota) and 4 specimens to *S roanensis* with 89% probability (10% to *S. sciaphila*; *Tenney 545* MIN from Winona Co., Minnesota; long internodes, few leaves), 71% probability (18% to *S. sciaphila* an 10% to *S. hispida*; *Dunevitz 693* MIN from Winona Co., Minnesota), 53% probability (40% to *S. sciaphila* and 6% to *S. hispida*; Hartley 9002 MIN from Debuque Co., Iowa), and 41% probability (36% to *S. sciaphila* and 22% to *S. hispida*; *Dunevitz 699* MIN from Winona Co., Minnesota). Fourteen of the 19 specimens of the *S. roanensis* a priori group (74%) were assigned a posteriori to the *S. roanensis* group: 1 specimen with 96% probability, 3 specimens with 81-84% probability, 5 specimens with 72-78% probability, 4 specimens with 51-59% probability, and 1 specimen with 47% probability (43% to *S. sciaphila*; *Cook et al. C-557* WAT from Haywood Co., North Carolina). Five specimens of the *S. roanensis* a priori group were assigned a posteriori to other groups: 2 specimens to *S. sciaphila* with 85% probability (13% to *S. roanensis*; *Poindexter 05-1580* BOON from Ashe Co., North Carolina) and 67% probability (30% to *S. roanensis*; *Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina); and 3 specimens to *S. hispida* with 79% probability (212), 62% probability (108), and 52% probability (Boone s.n.4 TAWES from Garrett Co., Maryland). Forty-two of the 76 specimens of the *S. hispida* a priori group (55%) were assigned a posteriori to the *S. hispida* group: 4 specimens with 91-94% probability, 5 specimens with 80-86% probability, 8 specimens with 70-78% probability, 13 specimens with 60-69% probability, 8 specimens with 51-59% probability, and 4 specimens with 38-48% probability). Thirty-four specimens of the *S. hispida* a priori group plus 1 specimen not assigned to an a priori group were assigned a posteriori to other groups: 17 to *S. bicolor* with 83-43% probability, 7 to *S. roanensis* with 91-48% probability, 7 to *S. sciaphila* with 93-36% probability, and 4 to *S. erecta* with 85-69% probability. Two specimens of var. *arnoglossa*, 20 specimens of var. *hispida*, 7 specimens var. *huronensis*, and 5 specimens var. *tonsa* were included among the 34 specimens of *S. hispida* assigned a posteriori to other species.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 150 specimens of *Solidago bicolor*, *S. erecta*, *S. hispida*, S. *roanensis*, and *S. sciaphila* are presented in Fig. 16. Eigenvalues on the first three axes were 1.148, 0.787 and 0.226.

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*erecta*	*hispida*	*roanensis*	*sciaphila*	% correct
bicolor	13	1	1	1	1	76
erecta	0	15	2	0	1	83
hispida	18	4	42	5	7	55
roanensis	0	0	3	14	2	74
sciaphila	0	1	0	4	15	75
Totals	31	21	48	24	26	66

Jackknifed classification matrix

Group	*bicolor*	*erecta*	*hispida*	*roanensis*	*sciaphila*	% correct
bicolor	13	1	1	1	1	76
erecta	0	15	2	0	1	83
hispida	18	4	42	5	7	55
roanensis	0	0	3	11	5	58
sciaphila	0	1	0	4	15	75
Totals	31	21	48	21	29	64

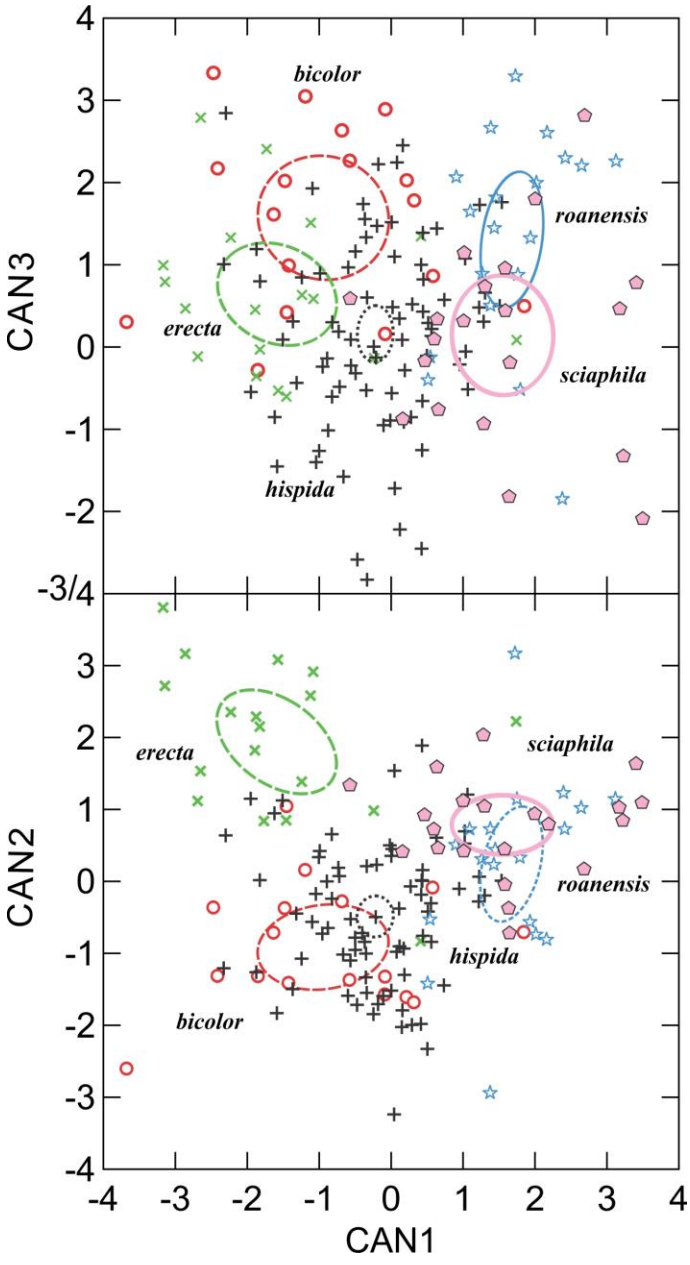

Figure 17. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 150 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Three species a priori groups analysis I

In the STEPWISE discriminant analysis of 59 specimens of three species level a priori groups (*S. bicolor*, *S. roanensis*, and *S. sciaphila*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (12.42), upper leaf length (11.59), ray floret lamina length (10.53), mid stem leaf width (9.96), number of ray florets (5.66), and involucre height (4.83). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. bicolor* and *S. sciaphila* (14.769), and the least separation was between *S. roanensis* and *S. sciaphila* (4.640).

Table 6. Between groups F-matrix for the three a priori groups analysis (df = 6 51).

Group	*bicolor*	*roanensis*
roanensis	7.528	
sciaphila	14.769	4.640

Wilks' lambda = 0.2713 df = 6 2 56; Approx. F= 7.8194 df = 12 102 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. bicolor*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 70-88%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. Fourteen of 16 specimens of the *S. bicolor* a priori group (88%) were assigned a posteriori to the *S. bicolor* group; 9 specimens with 91-100% probability, 3 specimens with 86-87% probability, and 2 specimens with 79% and 70% probabilities. Two specimens of the *S. bicolor* a priori group plus one not included in an a priori group were assigned a posteriori to *S. roanensis* with 84% probability (16% to *S. sciaphila*; *Hinds* 3826 from Cape Breton, Nova Scotia), 80% probability (15% to *S. bicolor* and 5% to *S. roanensis*; *Semple 10656* WAT from Leeds Co., Ontario), and 61% probability (31% to *S. bicolor* and 5% to *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Eighteen of the 23 specimens of the *S. sciaphila* a priori group (78%) were assigned a posteriori to the *S. sciaphila* group: 9 specimens with 91-96% probability, 5 specimens with 80-89% probability, 1 specimen with 76% probability; 2 specimens with 65-67% probability, and 1 specimen with 51% probability (49% to *S. roanensis*; *Semple 11851* WAT from Vernon Co., Wisconsin). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to the other groups: 3 specimens to *S. roanensis* with 90% probability (7% to *S. sciaphila*; *Semple 11854* WAT from Carroll Co., Illinois), 59% probability (41% to *S. sciaphila*; *Semple 11851* WAT from Vernon Co., Wisconsin), and 40% probability (31% to *S. sciaphila* and 29% to *S. bicolor*; *Dunevitz 911* MIN from Winona Co., Minnesota); and 2 specimens to *S. bicolor* with 54% probability (39% to *S. roanensis*; *Dunevitz 699* MIN from Winona Co., Minnesota), and 35% probability (33% to *S. sciaphila* and 32% to *S. roanensis*; *Dunevitz 978* MIN from Winona Co., Minnesota). Fourteen of the 20 specimens of *S. roanensis* a priori group (70%) were assigned a posteriori to the *S. roanensis* group; 3 specimens with 91-97% probability, 2 specimens with 88-89% probability, 3 specimens with 76-77% probability, 2 specimens with 68% and 60% probabilities, 2 specimens with 55% probability (44% to *S. sciaphila*, and 30% to *S. sciaphila* and 14% to *S. bicolor*, respectively), and 1 specimen with 46% probability (36% to *S. bicolor* and 19% to *S. sciaphila*; *Radford 6481* NCU from Macon Co., North Carolina). Six specimens of the *S. roanensis* a priori group were assigned to other species: 4 specimens to *S. sciaphila* with 89% probability (*Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina), 71% probability (*Cusick 25763* NY from Garrett Co., Maryland), 63% probability (*Biltmore Herb. 4622* NY), and 62% probability *(Cook et al. C-557* WAT from Haywood Co., North Carolina); and 2 specimens to *S. bicolor* with 55% probability (39% to *S. roanensis* and 7% to *S. sciaphila*; *Heller & Halbach 1178* NY from Augusta Co., Virginia) and 51% probability (48% to *s. roanensis*; *G. Morton 1747* NY from Giles Co., Virginia).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 59 specimens of *Solidago bicolor*, S. *roanensis*, and *S. sciphila* are presented in Fig. 18. Eigenvalues on the first two axes were 1.7439, and 0.344.

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*roanensis*	*sciaphila*	% correct
bicolor	14	2	0	88
roanensis	2	14	4	70
sciaphila	2	3	18	78
Totals	18	19	22	78

Jackknifed classification matrix

Group	*bicolor*	*roanensis*	*sciaphila*	% correct
bicolor	14	2	0	88
roanensis	3	11	6	55
sciaphila	2	5	16	70
Totals	19	18	22	69

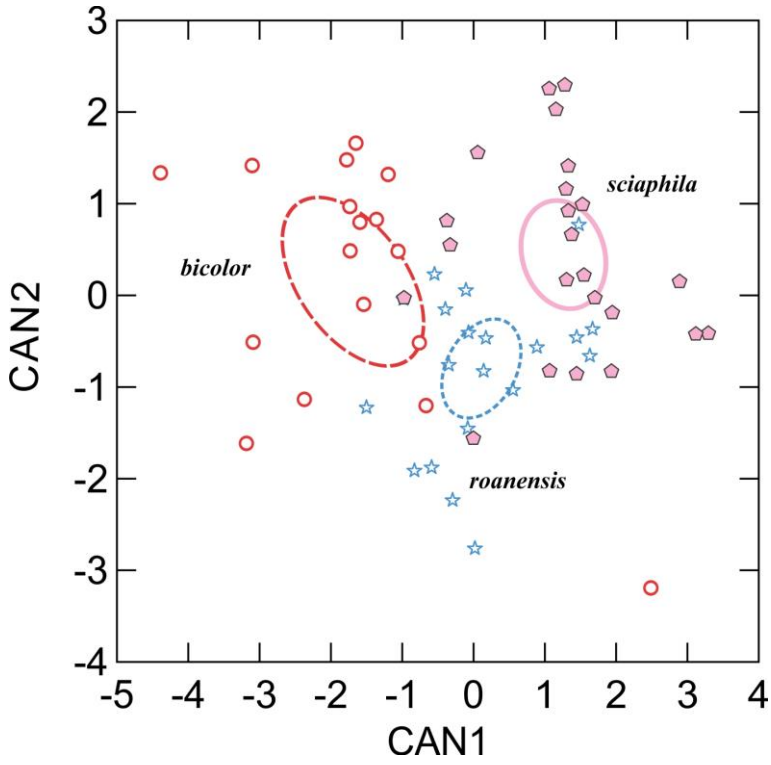

Figure 18. Plot of canonical scores (CAN1 vs CAN2) for 59 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Three species a priori groups analysis II

In the STEPWISE discriminant analysis of 112 specimens of three species level a priori groups (*S. bicolor*, *S. hispida* and *S. roanensis*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (20.21), mid stem leaf length (12.89), number of ray florets (7.66), ray achene body length (4.92), outer phyllary length (4.76), inner phyllary length (4.76), and ray floret lamina width (4.70). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all

groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 8. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. hispida* and *S. roanensis* (11.345), and the least separation was between *S. bicolor* and *S. hispida* (7.716).

Table 8. Between groups F-matrix for the three a priori groups analysis (df = 7 103).

Group	***bicolor***	***hispida***
hispida	7.716	
roanensis	11.226	11.345

Wilks' lambda = 0.3632 df = 7 2 109; Approx. F= 9.7029 df = 14 206 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. bicolor*, *S. hispida*, and *S. roanensis*), percents of correct a posterori assignment to the same a priori group ranged from 75-84%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Results are presented in order of decreasing percents of correct placement. Sixteen of 19 specimens of the *S. roanensis* a priori group (84%) were assigned a posteriori into the *S. roanensis* group; 13 specimens with 90-100% probability, and 2 specimens with 76% probability. Three specimens of the *S. roanensis* a priori group were assigned to *S. hispida* with 85% probability (14% to *S. roanensis*; *Boon s.n.-4* TAWES from Garrett Co., Maryland), 49% probability (40% to *S. roanensis* and 12% to *S. bicolor*; *Rydberg 8064* NY from Smyth Co., Virginia), and 49% probability (37% to *S. roanensis* and 13% to *S. bicolor*; *Radford 6481* NCU from Macon Co., North Carolina). Fifty-seven of the 76 specimens of the *S. hispida* a priori group (75%) were assigned a posteriori to the *S. hispida* group: 15 specimens with 90-98% probability, 15 specimens with 80-89% probability, 9 specimens with 70-79% probability, 9 specimens with 60-67% probability, 8 specimens with 53-58% probability, and 1 specimen with 45% probability (30% to *S. roanensis* and 24% to *S. bicolor*; *Morton & Venn NA12336* TRT from Northern Peninsula, Newfoundland; var. *arnoglossa*). Nineteen specimens of the *S. hispida* a priori group were assigned a posteriori to the other species: 10 yellow-rayed specimens were assigned a posterior to *S. bicolor* with 84% probability (12% to *S. hispida*; *Semple et al. 2987* WAT from Scioto Co., Ohio; sparsely very short strigose lower stem, moderately so in inflorescence), 81% probability (19% to *S. hispida*; *Semple & Brouillet 3638* WAT from Greene Co., New York), 79% probability (20% to *S. hispida*; *Morton NA6751a* TRT from Manitoulin Dist., Ontario), 71% probability (24% to *S. hispida*; *Oldham 37024* from Cochrane Dist., Ontario; var. aff. *huronensis*), 70% probability (30% to *S. hispida*; *Hall 693 AE-AF* MT from Thetford Mines, Québec), 65% probability (22% to *S. hispida* and 13% to *S. roanensis*; *Morton NA3978* WAT from Gaspésie, Québec), 64% probability (35% *S. hispida*; *Hall 829 DF* MT from Kingsbury, Québec), 64% probability (36% *S.* hispida; *Semple & B. Semple 11426* WAT from Gaspésie, Québec), 63% probability (26% *S. hispida* and 10% *S. arnoglossa*; *Cook & Tereszchuk C-156* WAT from Coos Co., New Hampshire), and 56% probability (44% to *S.hispida*; *Morton NA6656* TRT from Manitoulin Dist., Ontario); and 10 specimens including one added to the a posteriori sample were assigned a posterior to *S. roanensis* with 95% probability (*Morton & Venn NA12186* WAT from Table Mt., Newfoundland; var. *tonsa*), 75% probability (*Morton & Venn NA12186* TRT from Table Mt., Newfoundland; var. *tonsa*), 70% probability (29% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*), 67% probability (33% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*), 64% probability (25% to *S. hispida* and 11% to *S. bicolor*;

Morton & Venn NA12474 TRT from Blow-me-down Mts., Newfoundland; var. *arnoglossa*), 60% probability (21% to *S. bicolor* and 19% to *S. hispida*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland; var. *tonsa*), 60% probability (30% to *S. hispida* and 10% to *S. bicolor*; *Morton NA4086* TRT from the Gaspé, Québec; var. *tonsa*), 56% probability (44% to *S. hispida*; *Morton & Venn NA12438* TRT from Newfoundland, var. *tonsa*), and 52% probability (47% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*). Twelve of the 17 specimens of *S. bicolor* a priori group (71%) were assigned a posteriori to the *S. bicolor* group; 5 specimens with 94-100% probability, 4 specimens with 82-88% probability, and 3 specimens with 74-78% probability. Five specimens of the *S. bicolor* a priori group were assigned to the other species: 1 specimen to *S. roanensis* with 96% probability (*Semple 10656* WAT from Leeds Co., Ontario); and 4 specimens to *S. hispida* with 68% probability (20% to *S. bicolor* and 13% to *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island), 57% probability (43% to *S. bicolor*; *Semple & Keir 4797* WAT from Halifax Co., Nova Scotia), 57% probability (42% to *S. bicolor*; *Semple 10676* WAT from Greene Co., Pennsylvania), and 52% probability (47% to S. bicolor; *Oldham 22125* WAT from the Magdalen Is., Québec).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*hispida*	*roanensis*	% correct
bicolor	12	4	1	71
hispida	10	57	9	75
roanensis	0	3	16	84
Totals	22	64	26	76

Jackknifed classification matrix

Group	*bicolor*	*hispida*	*roanensis*	% correct
bicolor	11	5	1	65
hispida	10	57	9	75
roanensis	1	3	15	79
Totals	22	65	25	74

A two dimensional plot of CAN1 versus CAN2 canonical scores for 112 specimens of *Solidago bicolor*, *S. hispida*, and, S. *roanensis* is presented in Fig. 19. Eigenvalues on the first two axes were 0.830 and 0.505.

Three species groups analysis III

In the STEPWISE discriminant analysis of 85 specimens of three species level a priori groups (*S. hispida*, *S. sciaphila* and *S. speciosa*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (33.15), number of ray florets (13.07), outer phyllary length (13.34), mid stem leaf length (10.31), ray floret lamina length (9.72), disc corolla length (7.80), and inner phyllary length (4.50). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 10. F-values based on Mahalanobis

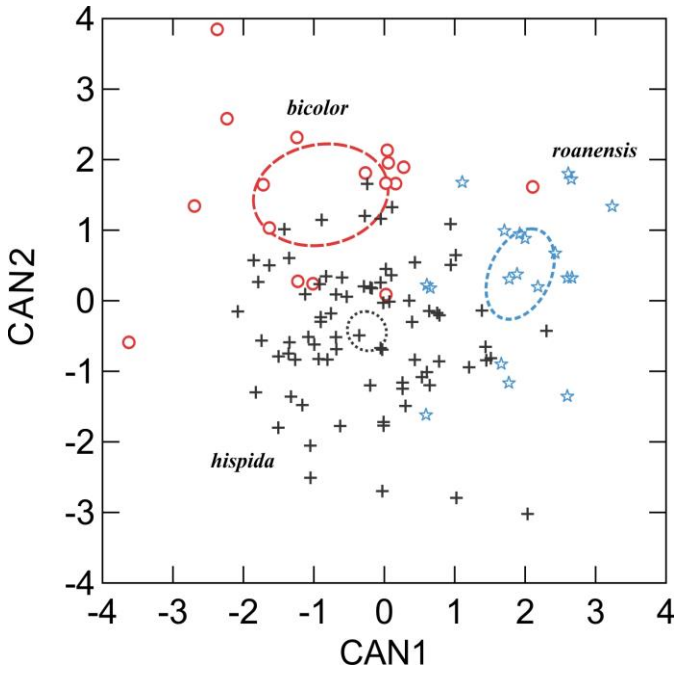

Figure 19. Plot of canonical scores (CAN1 vs CAN2) for 112 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. hispida* (black +s), and *S. roanensis* (open blue stars).

distances between group centroids indicated the largest separation was between *S. hispida* and *S. speciosa* (29.367), and the least separation was between *S. hispida* and *S. sciaphila* (13.014).

Table 10. Between groups F-matrix for the three a priori groups analysis (df = 7 76).

Group	***hispida***	***sciaphila***
sciaphila	13.014	
speciosa	29.367	22.687

Wilks' lambda = 0.1199 df = 7 2 82; Approx. F= 20.4951 df = 14 152 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. hispida*, *S. sciaphila* and *S. speciosa*), percents of correct a posterori assignment to the same a priori group ranged from 90-96%. The Classification matrix and Jackknife classification matrix are presented in Table 11. Results are presented in order of decreasing percents of correct placement. Twenty-two of 23 specimens of the *S. speciosa* a priori group (96%) were assigned a posteriori into the *S. speciosa* group; 18 specimens with 91-100% probability (13 with 100%), 2 specimens with 86% probability, and 1 specimen with 73% probability (27% to *S. sciaphila*). One specimen of the *S. speciosa* a priori group was assigned to *S. hispida* with 71% probability (29% to *S. speciosa*; *Semple & Chmielewski 6103* WAT from Lancaster Co., South Carolina; a 177 cm tall plant with mostly wilted lower stem leaves). Nineteen of the 20 specimens of the *S. sciaphila* a priori group (95%) were assigned a posteriori to the *S. sciaphila* group: 16 specimens with 90-100% probability, and 2 specimens with 83% probability, and 1 specimen with 46% probability (31% to *S. speciosa* and 23% to *S. hispida*; *Zager 930907-5* MIN from Houston Co, Minnesota; a 52 cm shoot with serrate lower and mid stem leaves and entire upper stem leaves). One specimen of the *S. sciaphila* a priori group

was assigned a posteriori to *S. speciosa* with 62% probability (27% to *S. sciaphila* and 11% to *S. hispida*; *Dunevitz 978* MIN from Winona Co. Minnesota; a 74 cm tall shoot with serrate large basal rosette and lower stem leaves and entire mid and much reduced upper stem leaves). Thirty-eight of the 42 specimens of *S. hispida* a priori group (75%) were assigned a posteriori to the *S. hispida* group (40 var. *hispida* and 2 var. *huronensis*); 32 specimens with 91-100% probability, 3 specimens with 81-89% probability, 1 specimen with 73% probability, and 2 specimens with 69% probability (17% to *S. sciaphila* and 14% to *S. speciosa*) and 62% (38% to *S. sciaphila*). Four specimens of the *S. hispida* a priori group were assigned to the other species: 3 specimens to *S. sciaphila* with 98% probability (2% to *S. hispida*; *Morton & Venn NA7682* WAT from Bruce Co., Ontario; a tall var. *huronensis* plant with glabrate stem), 98% probability (2% to *S. hispida*; *Hamel C68020* MT from the eastern townships of Québec; a 34 cm tall shoot with densely woolly stem), and 58% probability (41% to *S. hispida*; *Semple 9076* WAT from Douglas, Wisconsin; a 48 cm tall shoot with moderately hispid-villous stem and small mid and upper stem leaves); and 1 specimen to *S. speciosa* with 60% probability (35% to *S. hispida* and 5% to *S. sciaphila*; Morton *NA6656* WAT from Georgian Bay, Manitoulin Dist., Ontario).

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*hispida*	*sciaphila*	*speciosa*	% correct
hispida	38	3	1	90
sciaphila	0	19	1	95
speciosa	1	0	22	96
Totals	39	22	24	93

Jackknifed classification matrix

Group	*hispida*	*sciaphila*	*speciosa*	% correct
hispida	38	3	1	91
sciaphila	0	18	2	90
speciosa	1	0	22	96
Totals	40	21	25	92

A two dimensional plot of CAN1 versus CAN2 canonical scores for 86 specimens of *Solidago hispida*, *S. sciaphila* and *S. speciosa* is presented in Fig. 20. Eigenvalues on the first two axes were 2.813 and 1.187.

Two species a priori groups analysis of *Solidago hispida* and *S. bicolor*

In the STEPWISE discriminant analysis of 93 specimens of *S. bicolor* and *S. hispida*, the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper leaf width (19.12), disc floret pappus length at anthesis (18.70), inner phyllary length (18.05), and ray floret lamina length (8.93). The number of ray florets had the lowest F-to-remove value (0.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago bicolor* and *S. hispida* had an F-to separate value of 12.602 (Wilks' lambda = 0.6175 df = 4 1 91; Approx. F= 13.6296 df = 4 88 prob. 0.0000).

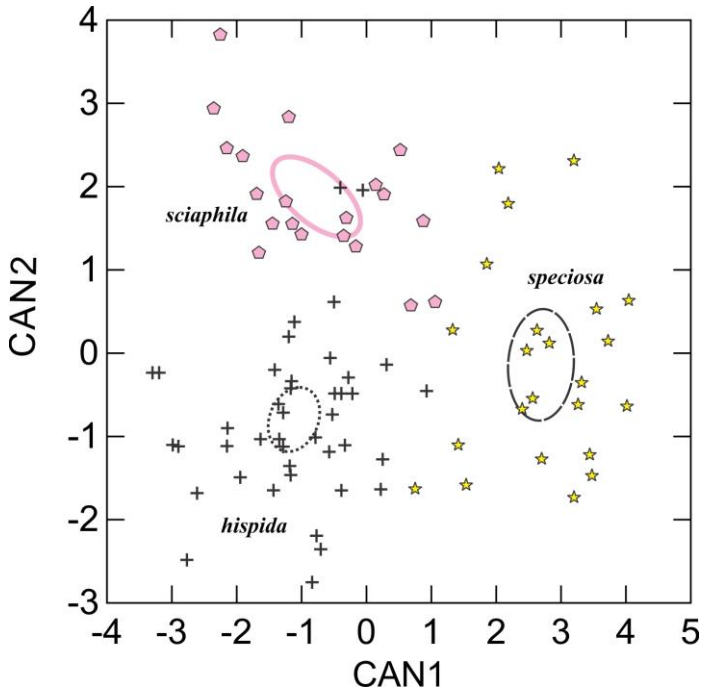

Figure 20. Plot of canonical scores (CAN1 vs CAN2) for 85 specimens of *Solidago hispida* (black +s), *S. sciaphila* (pink pentagons), and *S. speciosa* (yellow stars).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posterori assignment to the same a priori group were 88% for *S. bicolor* and 82% for *S. hispida*. Fifteen of the 17 specimens of *S. bicolor* were assigned a posteriori to *S. bicolor*: 10 specimens with 91-99% probability, 2 specimens with 81-82% probability, 1 specimen with 78% probability, and 1 specimen with 65% probability. Two specimens of the *S. bicolor* a priori group with white rays were assigned to *S. hispida*: with 79% probability (*Semple 10676* WAT from Greene Co., Pennsylvania) and 66% probability (*Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Sixty-two of the 76 specimens of *S. hispida* were assigned a posteriori to the *S. hispida* group: 40 specimens with 90-100% probability, 9 specimens with 80-89% probability, 5 specimens with 73-79% probability, 1 specimen with 64% probability, and 7 specimens with 51-59% probability. Fourteen specimens of the *S. hispida* a priori group with yellow rays were assigned a posteriori to *S. bicolor*: 5 specimens with 80-89% probability, 1 specimen with 72% probability, 5 specimens with 65-69% probability, and 2 with 56% and 55% probabilities.

Frequencies of CAN1 canonical scores for 93 specimens of *S. bicolor* and *S. hispida* are presented in histograms in Fig. 21. The Eigenvalue on the first axis was 0.620.

Table 12. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*hispida*	% correct
bicolor	15	2	88
hispida	14	62	82
Totals	29	64	83

Jackknifed classification matrix

Group	*bicolor*	*hispida*	% correct
bicolor	14	3	82
hispida	15	61	80
Totals	29	64	81

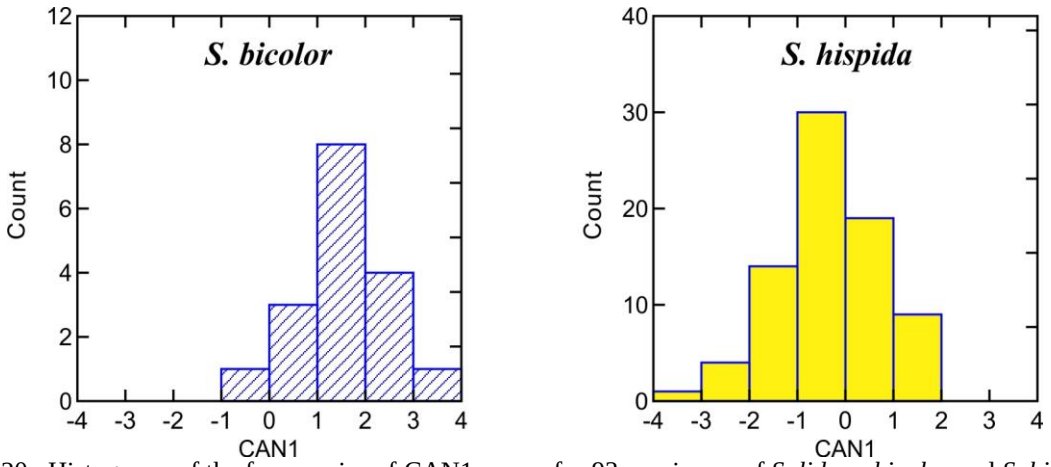

Figure 20. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago bicolor* and *S. hispida*.

Four variety level a priori groups analysis of *Solidago hispida* I

In the STEPWISE discriminant analysis not including stem height of 76 specimens of four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: outer phyllary length (14.87), number of ray florets (11.57), and disc floret pappus length at anthesis (9.62). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 13. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *hispida* and var. *tonsa* (18.503); the smallest separation was between var. *arnoglossa* and var. *hispida* (7.542).

Table 13. Between groups F-matrix for the four variety level a priori groups analysis of *S. hispida* (df = 3 70).

Group	*arnoglossa*	*hispida*	*huronensis*
hispida	9.715		
huronensis	12.750	10.063	
tonsa	7.542	18.5037	8.869

Wilks' lambda = 0.3189 df = 3 3 72; Approx. F= 11.3220 df = 9 170 prob = 0.0000

In the Classificatory Discriminant Analysis not including stem height of the four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*),

percents of correct a posterori assignment to the same a priori group ranged from 50-89%. The Classification matrix and Jackknife classification matrix are presented in Table 14. Results are presented in order of decreasing percents of correct placement. Eight of the 9 specimens of the var. *tonsa* a priori group (89%) were assigned a posteriori into the var. *tonsa* group; 4 specimens with 94-100% probability, 1 specimen with 87% probability, 1 specimen with 60% probability, 1 specimen with 55% probability (28% to var. *huronensis*, 9% to var. *arnoglossa*, and 8% to var. *hispida*; 186), and 2 specimens with 48% probability (*Morton NA4086* TRT from the Gaspé, Québec) and 40% probability (*Morton & Venn NA12186* TRT from Table Mt., Newfoundland). One specimen of the var. *tonsa* a priori group was assigned a posteriori to var. *huronensis* with 51% probability (24% to var. *hispida* and 22% to var. *tonsa*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland). Thirty of the 40 specimens of var. *hispida* a priori group (75%) were assigned a posteriori to the var. *hispida* group; 4 specimens with 90-93% probability, 7 specimens with 82-88% probability, 5 specimens with 70-79% probability, 5 specimens with 61-69% probability, 5 specimens with 56% probability (41% to var. *arnoglossa*; Hamel *C66206* MT from Thetford Mines, Québec), 56% probability (34% to var. *huronensis*, 5% to var. *arnoglossa*; *Morton NA3978* WAT from Bic Is., Gaspé, Québec), 54% probability (34% to var. *huronensis* and 11% to var. *arnoglossa*; *Baldwin 11554* WAT from Manitoba), 54% probability (35% to var. *arnoglossa*, 10% to var. *huronensis*; *Semple & B. Semple 6723* WAT from Kenora Dist., Ontario), and 53% probability (24% to var. *huronensis* and 22% to var. *arnoglossa*; *Semple & Bramall 2868* WAT from Algoma Dist., Ontario); and 4 specimens with 46% probability (44% to var. *huronensis*; *Doucet Do-59-7-3* MT from N of Coleraine, Québec), 46% probability (29% to var. *huronensis*, 13% to var. *arnoglossa*, and 13% to var. *tonsa*; *Hall 195 F* MT from Parq du Mont-Orford, Québec), 41% probability (41% to var. *arnoglossa* and 15% to var. *tonsa*; *Hall 795 BE* MT from St-Joseph-de-Coleraine Réserve écologique, Québec), and 32% probability (30% to var. *huronensis*, 26% to var. *arnoglossa*, and 12% to var. *tonsa*; *Doucet Do-59-7-5* MT from Black Lake, Québec; moderately densely woolly stem). Thirteen specimens of the var. *hispida* a priori group were assigned to other varieties: 7 specimens to var. *arnoglossa* with 79% probability (13% to var. *hispida* and 7% to var. *tonsa*; *Semple & Brammall 2818* WAT from Cochrane Dist., Ontario), 76% probability (20% to var. *hispida*; *Doucet Do-59-7-6* MT from Black Lake, Québec), 74% probability (16% to var. *hispida*; *Semple & Heard 8315* WAT from Fulton Co., Arkansas), 56% probability (31% to var. *hispida*; and 13% to var. *tonsa*; *Semple & Brammall 2846* from Sudbury Dist., Ontario), 50% probability (34% to var. *hispida* and 10% to var. *tonsa*; *Sauleda 4285* WAT from Rappahannock Co., Virginia), 49% probability (47% to var. *hispida*; *Semple & Brouillet 3638* WAT from Greene Co., New York), and 34% probability (34% to var. *tonsa*, 22% to var. *hispida* and 10% to var. *huronensis*; *Hall 5824 AI* MT from N of lac La Rauche, Québec); 5 specimens to var. *huronensis* with 85% probability (13% to var. *hispida*; *Semple 9076* WAT from Douglas Co., Wisconsin), 82% probability (16% to var. *hispida*; *Arnett & Hastings 1081* LSU from Rapides Par., Louisiana; moderately hispid-woolly stem), 78% probability (13% to var. *tonsa*; *Hamel C68020* MT from canton de Nelson, Québec), 66% probability (33% to var. *hispida*; *Semple & Suripto 9914* WAT from Oregon Co., Missouri), and 65% probability (25% to var. *tonsa* and 7% to var. *hispida*; *Thomas et al. 69272* WAT from Ashley Co., Arkansas; moderately dense long woolly hairs on stem); and 1 specimen to var. *tonsa* with 91% probability (7% to var. *arnoglossa*; *Morton & Venn NA12163* TRT from Gros Morne N.P., Newfoundland). Eight of the 11 specimens of the var. *huronensis* a priori group (73%) were assigned a posteriori to the var. *huronensis* group: 4 specimens with 93-96% probability, 1 specimen with 83% probability, 1 specimen with 62% probability, and 2 specimens with 57% probability (40% to var. *tonsa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario) and 52% probability (24% var. *arnoglossa* and 17% var. *hispida*; *Morton & Venn NA7682* WAT from Bruce Co., Ontario). Three specimens of the var.

huronensis group were assigned a posteriori to the var. *hispida* group with 75% probability (18% to var. *huronensis* and 6% to var. *arnoglossa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario), 71% probability (24% to var. *arnoglossa*; *Oldham 37024* WAT from Cockrane Dist., Ontario), and 61% probability (34% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Eight of 16 specimens of the var. *arnoglossa* a priori groups (50%) were assigned a posteriori to the var. *arnoglossa* group: 3 specimens with 93-97% probability, 1 specimen with 89% probability, 3 specimens with 71-77% probability, and 1 specimen with 66% probability. Eight specimens of the var. *arnoglossa* a priori group were assigned a posteriori to other varieties: 4 specimens to var. *hispida* with 84% probability (9% to var. *arnoglossa* and 7% to var. *huronensis*; *Morton & Venn* NA15322 TRT from Mistassini, Québec), 64% probability (19% to var. *huronensis* and 16% to var. *hispida*; *Morton* NA3978 TRT from Bic Is., Gaspé, Québec), 60% probability (33% to var. *arnoglossa*; *Morton & Venn* NA15322 TRT from Mistassini, Québec), and 52% probability (42% to var. *arnoglossa*; Morton s.n. TRT from Cap au Renaud, Gaspé, Québec); and 2 specimens to var. *huronensis* with 50% probability (23% to var. *hispida*, 19% to var. *tonsa*, and 9% to var. *arnoglossa*; *Morton & Venn NA12474* TRT from Blow-me-down Mts., Newfoundland; moderately woolly stem) and, 44% probability (25% to var. *tonsa*, 17% to var. *hispida*, and 14% to var. *arnoglossa*; *Morton s.n.* TRT

Table 14. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four variety level a priori groups in *S. hispida*; a posteriori placements to groups in rows.

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	8	4	2	2	50
hispida	6	30	3	1	75
huronensis	0	3	8	0	73
tonsa	0	0	1	8	89
Totals	14	37	14	11	71

Jackknifed classification matrix

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	8	4	2	2	50
hispida	7	29	3	1	73
huronensis	0	3	7	1	64
tonsa	1	0	1	7	78
Totals	16	36	13	11	67

from Bon Ami Pt., Gaspé. Québec; moderately hispid-woolly stem); and 2 specimens to var. *tonsa* with 42% probability (38% to var. *arnoglossa*,and 16% to var. huronensis; *Morton & Venn NA12336* TRT from the Northern Peninsula, Newfoundland; stem moderately densely woolly) and 40% probability (27% to var. *huronensis*, 20% to var. *arnoglossa*, and 12% to var. *hispida*; *Morton s.n.* TRT from Bon Ami Pt., Gaspé. Québec; moderately hispid-woolly stem).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 77 specimens of *var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* of *S. hispida* are presented in Fig. 21. Eigenvalues on the first three axes were 0.888, 0.594 and 0.075.

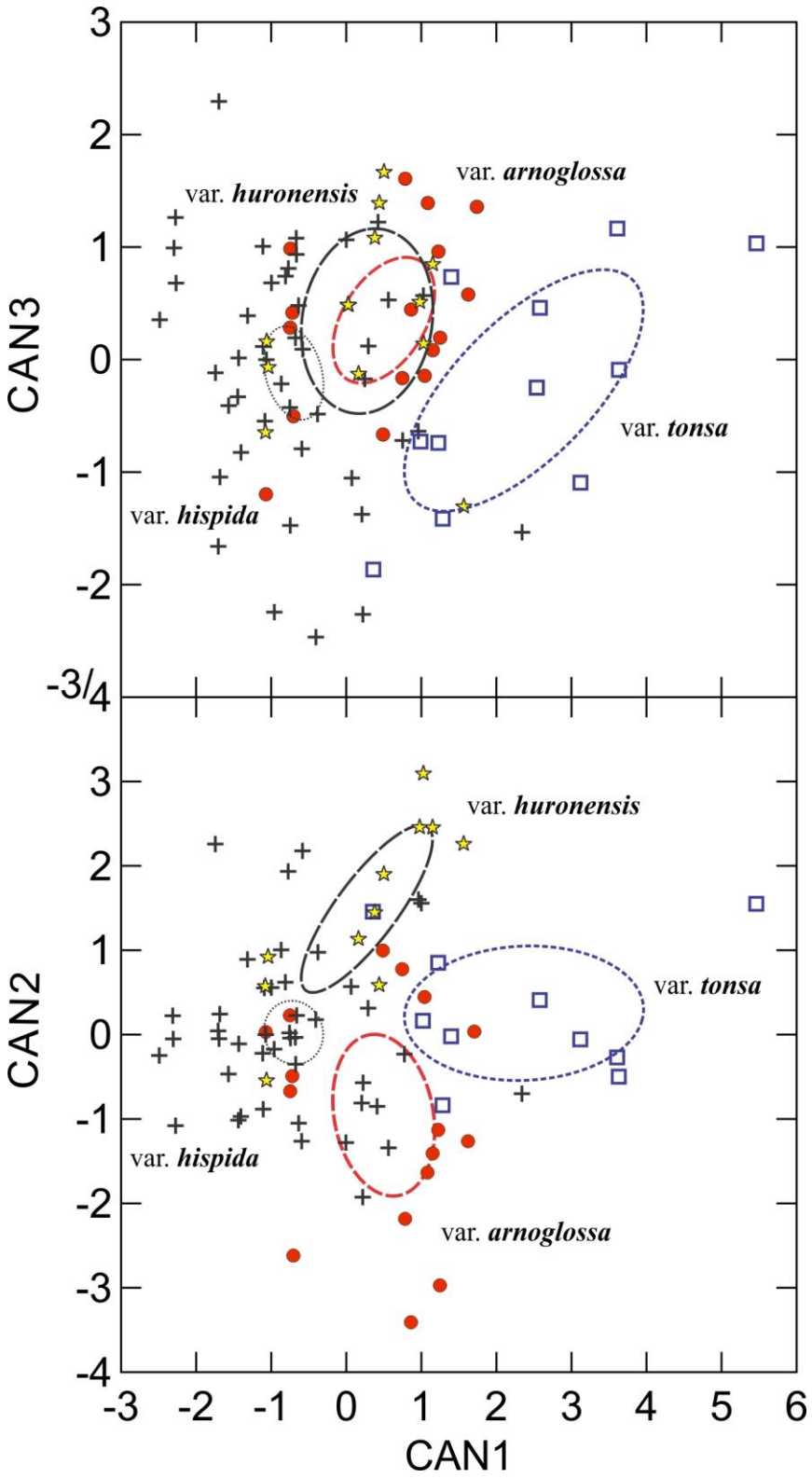

Figure 21. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 74 specimens of *Solidago hispida*, stem height not included in analysis: *var. arnoglossa* (red dots), var. *hispida* (black +s), var. *huronensis* (yellow stars), and *var. tonsa* (open blue squares).

Four variety level a priori groups analysis of *Solidago hispida* II

In the STEPWISE discriminant analysis including stem height of 74 specimens of four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (16.54), number of ray florets (10.75), outer phyllary length (9.17), disc floret pappus length at anthesis (7.17), and mid stem leaf length (3.34). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 15. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between var. *hispida* and var. *tonsa* (19.191) and var. *arnoglossa* and var. *hispida* (17.485); the smallest separations were between var. *arnoglossa* and var. *tonsa* (5.666) and var. *hispida* and var. *huronensis* (7.070).

Table 15. Between groups F-matrix for the four a priori group analysis of *S. hispida*, stem height included in the analysis (df = 4 67).

Group	*arnoglossa*	*hispida*	*huronensis*
hispida	17.485		
huronensis	15.257	7.070	
tonsa	5.666	9.191	10.803

Wilks' lambda = 0.2080 df = 4 3 70; Approx. F= 11.9533 df = 12 177 prob = 0.0000

In the Classificatory Discriminant Analysis including stem height of the four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), percents of correct a posterori assignment to the same a priori group ranged from 70-89%. The Classification matrix and Jackknife classification matrix are presented in Table 16. Results are presented in order of decreasing percents of correct placement. Eight of the 9 specimens of the var. *tonsa* a priori group (89%) were assigned a posteriori to the var. *tonsa* group; 5 specimens with 93-100% probability, 1 specimen with 74% probability, 2 specimens with 67% and 64% probabilities, 1 specimen with 51% probability (20% to var. *arnoglossa* 16% to var. *hispida* and 12% to var. *huronensis*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland). One specimen of the var. *tonsa* a priori group was assigned a posteriori to var. *arnoglossa* with 53% (46% to var. *tonsa*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland). Thirty-three of the 39 specimens of var. *hispida* a priori group (85%) were assigned a posteriori to the var. *hispida* group; 14 specimens with 90-99% probability, 6 specimens with 81-86% probability, 4 specimens with 70-79% probability, 1 specimen with 66% probability, and 6 specimens with 58% probability (41% to var. *huronensis*; *Boldwin 11554* WAT from Manitoba), 54% probability (26% to var. *huronensis*, 11% to var. *tonsa*, and 9% to var. *arnoglossa*; *Hall 195 F* MT from Parq du Mont-Orford, Québec), 53% (20% to var. *huronensis*, 16% to var. *tonsa*, and 12% to var. *arnoglossa*; *Hall 5824 AI* MT from N of lac La Rauche, Québec), 53% probability (44% to var. *huronensis*; *Doucet Do-59-7-3* MT from N of Coleraine, Québec), 51% probability (45% to var. *huronensis*; *Doucet Do-59-7-5* MT from Black Lake, Québec; moderately densely woolly stem), and 49% (32% to var. *arnoglossa* and 16% to var. *tonsa*; *Hall 795 BE* MT from St-Joseph-de-Coleraine Réserve écologique, Québec). Nine specimens of the var. *hispida* a priori group were assigned to other varieties groups: 5 specimens to var. *huronensis* with 91%

probability (9% to var. *hispida*; *Thomas et al 69272* WAT from Ashley Co., Arkansas), 87% probability (13% to var. *hispida*; *Arnett & Hastings 1081* LSU from Rapides Par., Louisiana), 86% probability (14% to var. *hispida*; *Semple 9076* WAT from Douglas Co., Wisconsin), 86% probability (6% to var. *hispida* and 6% var. *tonsa*; *Hamel C68020* MT from canton de Nelson, Québec), and 65% probability (35% to var. *hispida*; *Semple & Suripto 9914* WAT from Oregon Co., Missouri); 3 specimens to var. *arnoglossa* with 82% probability (10% to var. *hispida* and 4% to var. *huronensis*; *Semple & Brammall 2868* WAT from Algoma Dist., Ontario), 77% probability (14% to var. *hispida* and 7% to var. *tonsa*; *Semple & Brammall 2818* WAT from Cochrane Dist., Ontario), and 73% probability (17% to var. *hispida* and 6% to var. *huronensis*; *Semple & Keir 4659* WAT from Aroostock Co., Maine). Twelve of 16 specimens of the var. *arnoglossa* a priori groups (75%) were assigned a posteriori to the var. *arnoglossa* group: 5 specimens with 93-98% probability, 3 specimens with 81-86% probabilities, 1 specimen with 71% probability, 2 specimens with 59% probability (37% to var. *hispida* and 4% to var. *huronensis*; *Morton s.n.* TRT from Cap au Renaud, Gaspé, Québec) and 56% probability (35% var. *hispida* and 7% to var. *tonsa*; *Morton & Venn* NA15322 TRT from Mistassini, Québec), and 1 specimen with 47% probability (46% to var. *tonsa*; *Morton & Venn NA12336* TRT from Northern Peninsula, Newfoundland). Four specimens of the var. *arnoglossa* a priori group were assigned a posteriori to other varieties: 2 specimens to var. *tonsa* with 57% (28% to var. *arnoglossa* and 9% to var. *huronensis*; *Morton s.n*. TRT from Pt. Bon Ami, Gaspé, Québec) and 48% (27% to var. *arnoglossa*, 16% to var. *huronensis* and 9% to var. *hispida*; *Morton s.n*. TRT from Pt. Bon Ami, Gaspé, Québec); 1 specimen to var. *hispida* with 71% (20% to var. *huronensis* and 8% to var. *arnoglossa*; *Morton* NA3978 TRT from Bic Island, Gaspé, Québec), and 1 specimen to var. *huronensis* with 54% (31% var. *hispida* 11% var. *tonsa*; *Morton & Venn* NA12474 TRT from Blow-me-down Mts., Newfoundland). Seven of 10 specimens of var. *huronensis* a priori group (70%) assigned a posteriori to the var. *huronensis* group: 4 specimens with 97-98% probability, 1 specimen with 86% probability, 1 specimen with 77% probability, and 1 specimen with 55% probability (43% to var. *tonsa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Three specimens of the var. *huronensis* group were assigned a posteriori to the var. *hispida* group with 93% probability (7% to var. *huronensis*; *Oldham 37024* WAT from Cockrane Dist., Ontario), 80% probability (16% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario), and 65% probability (34% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 75 specimens of *var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* of *S. hispida* are presented in Fig. 22. Eigenvalues on the first three axes were 1.659, 0.630, and 0.110.

Table 16. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four varietal a priori groups in *S. hispida*, stem height included in the analysis; a posteriori placements to groups in rows.

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	12	1	1	2	75
hispida	2	33	3	1	85
huronensis	0	3	7	0	70
tonsa	1	0	0	8	89
Totals	15	37	11	11	81

Jackknifed classification matrix

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	10	2	1	3	63
hispida	3	33	3	1	83
huronensis	0	3	6	1	60
tonsa	1	0	0	8	89
Totals	34	38	10	13	77

DISCUSSION

Species level analyses

The results of the six species level multivariate analyses indicate that *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila* are distinct species. While the six species are for the most part morphologically similar, each has a diagnostic set of traits distinguishing it from the other five species. When traits often used in keys (e.g., ray floret color, stem hair density and distribution, and numbers of veins on the phyllaries) but not included in the analyses were considered, then most of the specimens that had been assigned a posteriori to a different group than each was assigned to a priori were easily assigned to their a priori groups. For example, all of the specimens of *S. bicolor* specimens had white rays even though some were assigned to other species using just the technical leaf and floral traits. All the specimens of *S. roanensis* had lower stems without hairs and increasingly more densely hairy stems distally, and most had multi-veined phyllaries but not all. There is considerable overlap in ranges of trait values among the species which resulted in a posterior miss assignments in the analyses that are not likely to happen using diagnostic traits not included in the analyses.

The results of the first analysis demonstrate that *Solidago porteri* has traits that strongly separate it from the other species. All specimens of *S. porteri* were assigned a posteriori to *S. porteri* with 96-100% probability. Difficulty in recognizing the species in the past has come mainly from lack of experience with the species because very few collections have been made by very few people. *Solidago porteri* is the only hexaploid taxon in *S.* subsect. *Squarrosae* (Semple and Estes 2014) and is most similar to species that are only known at the diploid level. The results of the multivariate study provide very little evidence as to which species (singular or plural) *S. porteri* is most closely related. In Fig. 17, symbols for specimens of *S. erecta* are closer to those of *S. porteri* on the CAN1 versus CAN2 plot, but symbols for the two species were strongly separated on the CAN1 versus CAN3 plot. Whether *S. porteri* is of allopolyploid origins or simply the result of autoploidy within a species that once included diploids and tetraploids cannot be resolved on the basis of morphology. Cronquist (1980) discussed the species known only at the time from the type collection under *S. hispida*.

The results of the five species analysis support the recognition of *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* as separate species. Symbols for *S. erecta* were nearly fully separated from symbols for other species in the CAN1 versus CAN2 plot in Fig. 17 and the 95% confidence ellipse was well separated from the confidence ellipses for the other species. Based on F values between group centroids, *S. bicolor* and *S. hispida* (5.328) and *S. roanensis* and *S. sciaphila* (3.110) are the two most similar pairs of species, at least in terms of the traits selected to separate taxa in the five species analysis. Symbols for *S. bicolor* and *S. hispida* were mostly separated from symbols for *S. roanensis* and *S. sciaphila* in the CAN1 versus CAN2 diagram, but the confidence limits for the latter two species overlapped on these two axes much more than they did on the CAN1 versus CAN3 axes. Diagnostic differences in stem indument density and distribution and number of veins on the phyllaries were not included as traits in the analyses. When these traits are included then

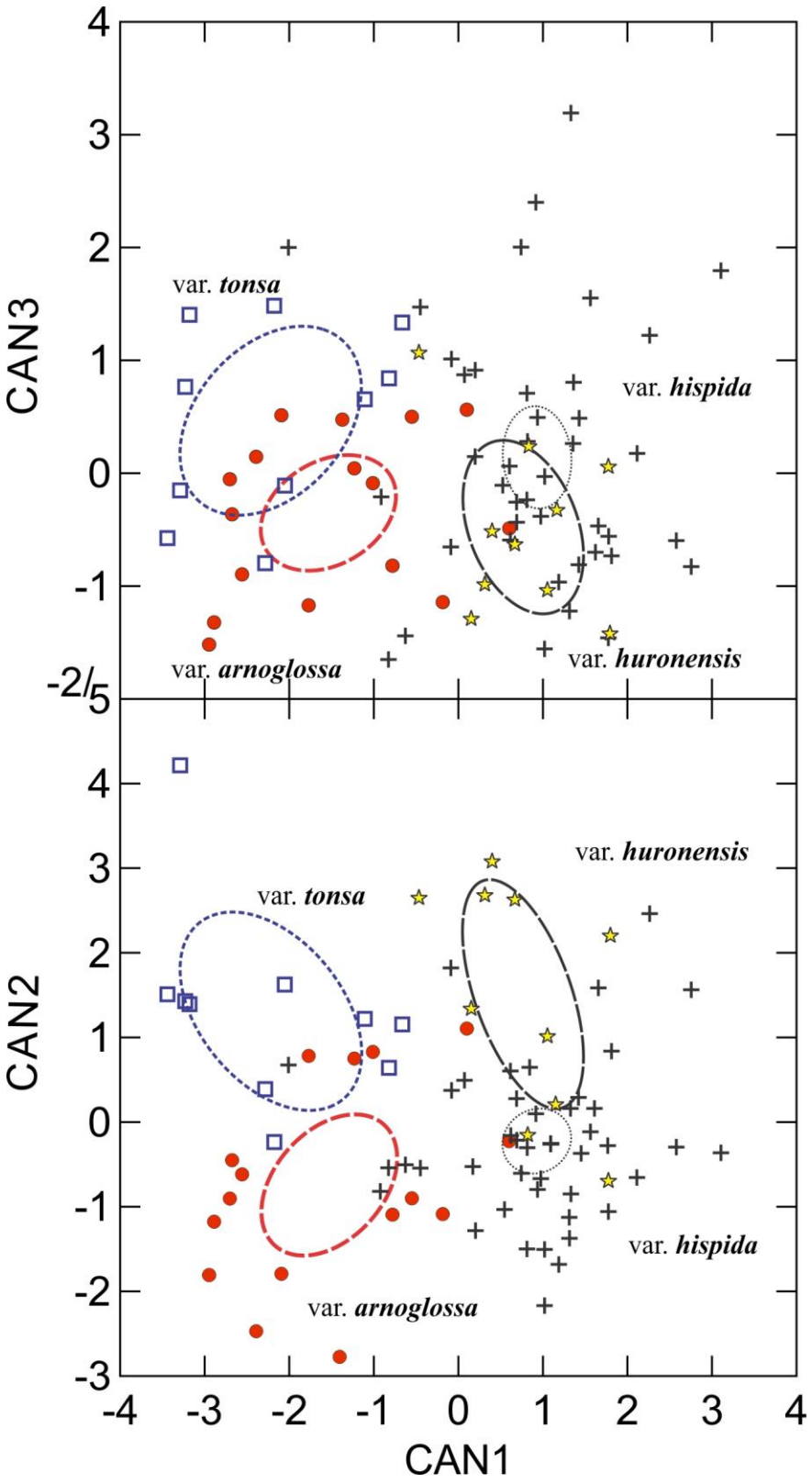

Figure 22. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 75 specimens of *Solidago hispida*, stem height included in the analysis: *var. arnoglossa* (red dots), var. *hispida* (black +s), var. *huronensis* (yellow stars), and *var. tonsa* (open blue squares).

S. roanensis and *S. sciaphila* are much easier to distinguish. The ranges of the two species are fully allopatric; both species occur in Illinois but *S. roanensis* is confined to the southern areas of the state while *S. sciaphila* occurs only in the northwestern corner of the state. Neither occurs in the flat prairies portion of Illinois.

The glabrous lower and mid stems of *Solidago erecta* usually make the species easily distinguished from the other species in the *S. bicolor* complex. The glabrous and glabrate stem varieties of *S. hispida* occur north or the range of *S. erecta*. Lower and mid stems of *S. erecta* are hairless while some hairs occur on stems and peduncles in the inflorescence. Mid and upper stems of *S. roanensis* are much hairier than those of *S erecta,* which is more likely to be confused with diploid plants of *S. speciosa* than with plants of the *S. bicolor* group of species. *Solidago erecta* usually has smaller leaves and shorter stems than *S. speciosa*, and large inflorescences of the former are more open and have shorter branches than the latter. Stem height in *Solidago* is a plastic trait greatly influenced by growing conditions. The field experience of the first author over many years indicates that when *S. speciosa* and *S. erecta* occur together, the smaller plants are always *S. erecta*.

The obvious field character difference between white rayed *Solidago bicolor* and yellow rayed *S. hispida* is not always discernable on herbarium specimens, particularly those that are old or were collected with heads past blooming. Plants of the two species collected in fruit can be challenging to place to species. The ranges of the two species are sympatric over much of the range of *S. bicolor* eliminating geography as helpful in determining which of the two species one has in hand. Fernald (1950) used a difference in phyllary traits as a secondary character to separate *S. bicolor* and *S. hispida*; phyllaries of *S. bicolor* purportedly had a more contrasting color difference between the green tip and the whitish to straminous bases and margins, while phyllaries of *S. hispida* had less contrasting color differences. Our examination of phyllaries of herbarium collections of the two species did not confirm this to be a reliable character, although some of the *S. bicolor* specimens had narrower zones of green pigmentation which might lead to the impression that the phyllaries of *S. bicolor* had a more obvious green to white contrast than on phyllaries of *S. hispida*. Differences in drying techniques and the age of specimens could also influence such color pattern differences. A preliminary observation that there might be a difference in degree of clavateness of the long inner pappus bristles resulted in the detailed investigation of pappus variation in the entire genus *Solidago*, but also resulted in the conclusion that *S. hispida* and *S. bicolor* had similarly moderately clavate long inner bristles (Hood & Semple 2003). In the two species a priori group analysis of *S. bicolor* and *S. hispida*, the technical traits of upper leaf width, inner phyllary length, disc floret pappus length at anthesis, and ray floret lamina length were selected to separate the two species with 81% and 84% of the specimens, respectively being assigned a posteriori to their a priori group (see Table 15) without using ray floret color.

In the *Solidago bicolor-S. roanensis-S. sciaphila* analysis, all three specimens of *S. bicolor* assigned to the other species groups a posteriori were from portions of the range of *S. bicolor* well outside the ranges of *S. roanensis* and *S. sciaphila*. All three had white rays. Clearly, these were specimens with atypical values for the traits used to separate the taxa in the STEPWISE analysis (disc floret pappus length, upper leaf length, and ray floret lamina length) and were not previously unrecognized members of species not known to be present in Ontario, Nova Scotia or Prince Edward Island.

Solidago sciaphila can be confused with *S. hispida* and *S. speciosa*. It has the most serrations on mid and upper stem leaves of any of the three species, but the leaves can be entire. The results of the three species analysis of specimens of *S. hispida*, *S. sciaphila*, and *S. speciosa* strongly support recognition of the three species with high probability of correct assignment and placement. Nonetheless, some collections from areas where the ranges of the three species are sympatric can be

difficult to assign to species. Tall plants of *S. sciaphila* from wooded slopes with loamy soil are the most likely to be confused with the generally much taller *S. speciosa*. In the analysis of the three species, the specimens of *S. hispida* assigned to *S. sciaphila* and *S. speciosa* came from parts of the range of *S. hispida* that are not sympatric with either species and had stem hair traits that would place them in *S. hispida*. The one collection of *S. speciosa* (*Semple & Chmielewski 6103* WAT, Lancaster Co., South Carolina) that was assigned in the three species analysis to *S. hispida* with 72% probability came from the edge of the Piedmont where *S. hispida* does not occur; also the specimen was 177 cm tall which is more than double the average height of *S. hispida*. In the study of the *S. speciosa* complex reported by Semple et al. (2017), *Semple & Chmielewski 6103* WAT was placed in *S. erecta* with 60% probability in the 14 species analysis, into *S. erecta* with 80% probability in the *S. speciosa-S. erecta-S. rigidiuscula* analysis, and into *S. speciosa* with 98% probability in the *S. jejunifolia-S. pallida-S. rigidiuscula-S. speciosa* analysis. The specimen is much too tall at 177 cm to be *S. erecta*. This, of course, is the challenge of working with *Solidago*. The specimen was annotated as *S. rigidiuscula* in 2012 by the first author, but the results of the analyses do not support that conclusion. Unfortunately, some individuals of *Solidago* can have atypical traits for the species they are members of and show technical affinities to species well outside their provenance or have other traits that are even more atypical for the other species. Alternative methods for assigning such specimens to a species are needed for those cases when correct identification is critical.

Solidago sciaphila is the only tetraploid in the *S. bicolor* complex. It is the only upper Midwestern USA endemic in the complex. Its range is much of the Driftless area of southeastern Minnesota, southwestern Wisconsin, and adjacent Illinois and Iowa, which was unglaciated during the last glaciation that peaked some 25,000 years ago. If not a refugial area for *S. hispida* like plants at peak glaciation, the area certainly would have been recolonized earlier than areas to the north and east and thus might have provided conditions favoring divergence into a distinct new taxon that is the only tetraploid species in the *S. bicolor* complex. It is unknown whether it is the result of autopolyploidy and subsequent loss of the diploid ancestors or the result of allopolyploidy involving two diploid parent species.

Data on character trait ranges and means for *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* are summarized in Table 15. The means are based on all raw scores for each character. Only mean values were used in the analyses. The data is only for specimens included in the analyses and more extreme values for numbers and sizes of parts will likely be encountered. Ovary/fruit traits were measured on florets from flowering heads and do not represent mature fruit values. A detailed description of *S. porteri* was included in Semple & Estes (2014).

Table 15. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. bicolor*, *S. erecta*, *S. hispida*, *S.* roanensis, and *S. sciaphila*: min-**mean**-max; * traits selected in STEPDISC analyses. Abbreviations of traits are described in Table 1.

Trait	***S. bicolor***	***S. erecta***	***S. hispida***	***S. roanensis***	***S. sciaphila***
STEMHT cm	15–**59**–104	53–**80**–116	5–**39.4**–100.5	**26–61.2–101**	19–**51.6**–77.7
BLFLN mm	22–**92.8**–180	97–**132**–164	7–**70.9**–175	**9.5–93.3–185**	30–**131.6**–290
BLFPETLN mm	6–**41.4**–101	40–**43.2**–50	2.7–**29.3**–85	**4.5–48.8–110**	16–**46**–120
BLFWD mm	7–**18.5**–35	19–**29**–40	1.5–**17.9**–52	**2.3–20.4–36**	19–**38.1**–68
BLFWTOE mm	8–**22.9**–45	15–**33**–40	1–**17.6**–55	**2.3–25.9–80**	16–36.6–65
BLFSER	0–**8.5**–29	0–**2.4**–6	0–**6.3**–23	**4–10.2–21**	2–**10.4**–19
LLFLN mm	26–**103**–159	42–**80.5**–144	7.7–**62.3**–157	10.5–**85.6**–150	42–**98.5**–175
LLFWD mm	6–**23.8**–43	7.5–**16.9**–39	1.7–**16.3**–50	2.4–**20.9**–42	14–**32.2**–55

LLFWTOE mm	10–**34.2**–62	10–**26.8**–78	2–**18.7**–50	3.4–**31.5**–55	15–**34.5**–60
LLFSER	0–**8**–17	0–**5.4**–26	0–**6.2**–28	5–**11.1**–20	2–**10.7**–19
MLFLN mm	12–**63.2**–123	22–**50.9**–87	3–**42.5**–102	7–**64.8**–125	10–**55.9**–115
MLFWD * mm	2–**15**–27	5–**10.4**–20	1.5–**11.3**–72	2–**16.3**–32	7–**19.6**–46
MLFWTOE mm	6–**27.3**–65	7–**21.7**–37	1.5–**16.6**–118	2.9–**31.2**–55	11–**25.5**–57
MLFSER*	0–**6.1**–16	0–**2.8**–14	0–**4.3**–17	1–**7.7**–20	0–**5.3**–17
ULFLN* mm	13–**40**–65	12–**28.3**–57	1.6–**28.5**–67	4–**39.9**–81	15–**33.8**–95
ULFWD* mm	3–**10.4**–19	2–**5.5**–13	0.6–**7**–18	1–**9.4**–19	3–**9.8**–32
ULFWTOE mm	6–**18.7**–35	4–**11.5**–31	0.7–**11.3**–35	2–**20.1**–41	6–**14.3**–40
ULFSER	0–**3**–13	0–**0.5**–7	0–**1.1**–8	0–**4.2**–14	0–**1.7**–10
CAPL cm	5.5–**21.4**–47	8.4–**25.8**–72	2.3–**14.6**–56	5.2–**16.4**–29.2	5.8–**14.3**–10
CAPW cm	1.5–**5.5**–20	1.5–**4**–12.8	1–**3.1**–27	1.8–**2.8**–7	1.3–**3.5**–16
INVOLHT* mm	2.6–**4.1**–6	3.2–**4.4**–6	2.5–**4.4**–6.5	2.3–**3.9**–5.6	3.1–**4.4**–6
OPHYLN* mm	0.9–**1.4**–2.1	1–**1.7**–2.5	0.75–**1.6**–3	0.5–**1.6**–2.8	1.1–**1.8**–2.8
IPHYLN* mm	1.9–**3.2**–4.5	2.4–**3.6**–4.8	1.2–**3.5**–4.8	2.1–**3.4**–4.8	2.5–**4.0**–5.2
RAYNUM*	3–**8**–15	4–**6.5**–10	3–**8.3**–16	2–**6**–13	3–**6.7**–14
RLAMLN* mm	1–**1.9**–2.7	1.4–**2.8**–4	0.5–**2.1**–3.5	1–**1.9**–3	1.5–**2.1**–3.2
RLAMWD* mm	0.15–**0.5**–1.1	0.2–**0.76**–1.9	0.1–**0.68**–1.5	0.4–**0.73**–1.6	0.3–**0.7**–1.2
RACHLN* mm	0.6–**1.4**–2.5	0.85–**1.6**–3.3	0.3–**1.3**–2.4	0.5–**1.2**–2.1	0.7–**1.6**–2.7
RPAPLN mm	1.8–**2.9**–3.8	1.9–**3.4**–5	1.1–**2.7**–4.2	1.3–**2.3**–3.1	1.3–**2.3**–3.3
DISCNUM	5–**10.5**–16	4–**9.5**–15	3–**10**–24	4–**8.6**–13	1–**8.7**–15
DCORLN mm	3–**3.9**–5.1	1.8–**4.4**–7.4	2.2–**4.2**–5	2.5–**3.6**–4.9	2.3–**3.7**–6.5
DLOBLN mm	0.3–**0.81**–1.5	0.25–**0.7**–1	0.2–**0.9**–1.5	0.2–**0.8**–1.7	0.2–**0.84**–1.2
DACHLN mm	0.7–**1.4**–2.5	0.9–**1.6**–3.1	0.5–**1.3**–2.5	0.6–**1.2**–2.3	0.8–**1.5**–2.6
DPAPLN* mm	1.9–**3.3**–4.4	2.5–**4**–5	1.2–**3.3**–5	1.5–**2.8**–4.2	2–**3**–4.3

Analyses of varieties of *Solidago hispida*

Fernald (1908, 1915) proposed four varieties in *Solidago hispida* – var. *arnoglossa*, var. *disjuncta*, var. *lanata*, and var. *tonsa* – which he stated were "well marked". The holotypes of var. *arnoglossa*, var. *disjuncta*, and var. *tonsa* are all from within about 30 km of Corner Brook, Newfoundland in different habitats. The type of var. *disjuncta* (*Fernald, Wiegand & Kittredge 4071*; holotype: GH!; isotypes: NY!, US on line image!) is a small plant with a densely woolly stem and may be nothing more than a dwarf individual of the "var. *lanata*" extreme indument morph or var. *hispida*; no densely woolly-stemmed plants from Newfoundland were included in the sample of var. *hispida* in this study. The type of var. *arnoglossa* is (*Waghorne s.n.*, holotype: GH!) includes two shoots about 34 cm tall, lower stems that are moderately hispidulo-strigose, and a basal rosette with the largest leaf about 12 × 5 cm with crenulo-serrate margins. The type of var. *tonsa* (*Fernald & Wiegand 4075*, holotype: GH!) includes five shoots 19-49 cm tall, stems that are very sparsely to sparsely woolly, and lower stem leaves that vary noticeably between shoots in margin serration size but are generally oblanceolate and acute. The smaller lowest leaves are subspathulate, obovate, and obtuse to rounded, which is a common in many species of *Solidago*.

The two analyses of the varieties of *Solidago hispida* indicate that there are differences among var. *arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* but that the varieties are not strongly separated and intermediates occur. Further research is needed to fully assess the usefulness

of recognizing these varieties. In the analysis without stem height included as a trait, outer phyllary length, numbers of ray florets, and disc floret pappus length were selected as discriminating traits, but only 50% of the specimens of var. *arnoglossa* were placed a posteriori into var. *arnoglossa*. In the second analysis with stem height included, stem height along with outer phyllary length, numbers of ray florets and disc floret pappus length were selected to separate taxa; 75% of the specimens of var. *arnoglossa* were placed a posteriori into var. *arnoglossa*. Thus, stem height is critical in separating var. *arnoglossa* from var. *tonsa*. The same was true in the case of var. *hispida* for which 76% of specimens in the first analysis were assigned a posteriori to var. *hispida*, but 85% in the second analysis with stem height included. However, the shortest specimen of var. *hispida* (*Semple & Brammall 2864* WAT; 13.8 cm tall stem shoot growing on Gneiss shoreline rocks of Lake Superior, Algoma Dist., Ontario) was assigned a posteriori to var. *hispida* with 53% probability in the first analysis (24% to var. *huronensis*), but in the second analysis when stem height was included as a trait the specimen was assigned a posteriori to var. *arnoglossa* with 82% probability (10% to var. *hispida*). Inclusion of stem height had little effect overall with placement in var. *huronensis* dropping from 73% a posteriori placement to var. *huronensis* in the first analysis to 70% in the second analysis. As noted above, stem height is a highly plastic trait in *Solidago* greatly influenced by growing conditions from one season to the next and by soil richness and moisture content. Stem height did not correlate strongly with other characters in any of the analyses done on members of subsect. *Squarrosae*, although generally smaller plants had small leaves. Var. *tonsa* is from habitats that likely result in stunted growth. Transplant studies would be useful in determining whether stem height is genetically limited or just a consequence of habitat growing conditions in this case. The var. *tonsa* appears to be a genetically based ecotype, but this needs confirmation.

The more northern shorter collection from Newfoundland included in the var. *hispida* a priori group (*Morton & Venn NA12163* TRT) was placed a posteriori into var. *tonsa* in both analyses with high probability (91% and 93%). The southern two taller shoots from Newfoundland included in the var. *hispida* a priori group (*Morton & Venn NA12438* TRT) were placed a posteriori into var. *hispida* in both analyses with high probability (87% and 75% in the analysis without stem height and 94% and 90% in the analysis with stem height included). Thus in these latter two cases stem height was not critical in the a posteriori placement of the var. *hispida* specimens from Newfoundland; the short plant went to var. *tonsa* even when stem height was not included. Stem hair density was similar and moderately dense in both of the collections and mid-range for var. *hispida* but high for var. *tonsa*. A larger sample size of var. *hispida* plants from Newfoundland is needed to further explore differences between var. *hispida* and var. *tonsa* in Newfoundland.

Results are ambivalent about the identity of the four specimens treated as var. *arnoglossa* from central and eastern Québec (3 shoots, *Morton & Venn* NA15322 TRT from Mistassini, Québec; 1 shoot *Morton* NA3978 TRT from Bic Island, Gaspé, Québec; red dots on map in Fig. 11). In the first analysis without stem height included, these specimens were assigned a posteriori in the analysis to var. *arnoglossa* with 71% probability (shoot #2, *Morton & Venn* NA15322 TRT) and to var. *hispida* with 84% (*Morton* NA3978 TRT), 64% and 60% (shoot #1 and shoot #3, *Morton & Venn* NA15322 TRT). In the analysis with stem height included as a discriminating trait, the four specimens were assigned a posteriori to var. *arnoglossa* with 96% (shoot #2, *Morton & Venn* NA15322 TRT; 23 cm tall), 82% (shoot #3, *Morton & Venn* NA15322 TRT; 19 cm tall) and 56% (shoot #1, *Morton & Venn* NA15322 TRT; 15 cm tall) and to var. *hispida* with 71% probability (*Morton* NA3978 TRT; 40 cm tall). Stem height was significant in placing the specimens to variety. The Bic Island collection was very sparsely hairy on the leaves and stems, while the Mistassini collections were moderately villous on the stem and strigose on the basal leaves. The short Mistassini plants are more likely just short members of var. *hispida*. The Bic Is., Gaspé plant is likely a less hairy member of var. *hispida*. A larger sample size of *S. hispida* from the eastern Gaspé and from all of Newfoundland is need to explore how distinct var. *arnoglossa* is from var. *hispida*.

As treated here, var. *hispida* includes plants with a wide range of variation in stem pubescence ranging from densely long-woolly ("var. *lanata*") to sparsely hispid-woolly (Figs. 4 A-D). Also included was a plant with canescent stems that had short strigose hairs (*Baldwin 11518* WAT from Saskatchewan; Fig. 4E). If the densely long-woolly morph is recognized as a separate variety, then the short-canescent morph should also possibly be recognized as a distinct variety. Our observations on stems indicated that the densely-woolly morph is just an extreme in a continuum of hair density and length. We did not include sufficient numbers of variously canescent stemmed plants in this study to reach a similar conclusion. A detailed study of stem hair density and length would be a useful analysis to clarify the range of variation on short-haired stems in *Solidago hispida* including more samples from Saskatchewan and Newfoundland. *Solidago hispida* is the only species in the *S. bicolor-S. hispida* complex with multiple varieties. A DNA based analysis of the distribution of distinct haplotypes and how these correlate with proposed varieties would also be useful, if sufficient variation in DNA sequence data occurs in the species.

Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis the varieties of *Solidago hispida* are presented in Table 16. Values in the table are only from the specimens included in the multivariate analyses. More extreme values for minimum and maximum for each trait for each species are likely to be encountered. Ovary/fruit values were taken from florets of heads in bloom. Mature fruits are bigger with longer pappus bristles.

Table 16. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis the varieites of *S. hispida*: min-**mean**-max. No data for basal leaves of *S. rigidiuscula* at flowering. The lowest stem leaves are also generally absent by flowering. * traits selected in STEPDISC analyses.

Trait	var. ***arnoglossa***	var. ***hispida***	var. ***huronensis***	var. ***tonsa***
STEMHT* cm	5–**20.5**–40.4	11.5–**50**–100.5	26–**43**–66	7–**16.1**–30.7
BLFLN mm	30–**70**–135	7–**79.8**–175	30–**70**–145	21–**40.8**–79
BLFPETLN mm	12–**31.8**–75	2.7–**31.6**–80	8–**31.4**–85	7–**20.1**–79
BLFWD mm	7–**17.7**–36	1.5–**19.9**–50	10–**19**–31	5–**10.6**–17
BLFWTOE mm	5–**15.2**–40	1–**21.5**–55	10–**19.7**–7.5	4–**8.6**–17
BLFSER	0–**5.7**–12	0–**7.6**–28	3–6.4–15	3–**5.3**–10
LLFLN mm	10–**49.9**–95	7.7–**67**–157	27–**66.9**–137	19–**47.7**–70
LLFWD mm	5–**11.6**–25	1.7–**17.9**–50	8–**18.3**–37	6–**11.7**–18
LLFWTOE mm	3–**11**–27	2–**21.5**–50	8–**21.8**–37	5–**10.1**–16
LLFSER	0–**4**–10	0–**7.6**–28	2–**9.3**–25	2–**6**–9
MLFLN mm	20–**41.9**–80	4–**45**–92	14–**34.1**–102	19–**43.4**–69
MLFWD mm	3–**10.7**–21	1.5–**12.2**–72	3–**9.5**–30	3–**9.3**–17
MLFWTOE mm	5–**10.9**–20	1.5–**19.3**–50	6–**14.8**–32	5–**11.1**–20
MLFSER	0–**3**–9	0–**4.4**–17	0–**4**–16	0–**5.5**–9
ULFLN mm	16–**32.8**–57	1.6–**29.5**–67	7–**19.1**–58	11–**31.3**–61
ULFWD mm	3–**8.1**–15	0.6–**7.2**–16	2–**5**–18	2–**6.5**–12
ULFWTOE mm	4–**9.8**–19	1–**12.6**–35	2–**9**–23	3–**9.2**–20
ULFSER	0–**1.2**–6	0–**0.9**–8	0–**1.3**–5	0–**1.9**–6
CAPL cm	2.5–**10.5**–22	4.5–**18.2**–56.5	5–**12.4**–27.3	2.3–**7.5**–17
CAPW cm	1.6–**2.5**–4.7	1–**3.1**–8.1	1.4–**4.9**–27	1.2–**1.9**–3.6
INVOLHT mm	3.2–**4.5**–5.3	2.5–**4.3**–6.5	3–**4.5**–5.9	2.5–**4.6**–6.5
OPHYLN* mm	0.75–**1.8**–2.5	0.85–**1.3**–2.1	0.9–**1.6**–2.2	0.9–**1.9**–3

IPHYLN mm	2.5–**3.8**–4.7	2.3.–**3.5**–4.8	1.2–**3.5**–4.8	2.1–**3.2**–3.9
RAYNUM*	4–**9.8**–16	3–**8**–14	3–**8**–14	5–**9.1**–14
RLAMLN mm	1.5–**2.4**–3.3	1.5–**2.1**–3.5	1–**2.1**–3.5	1.2–**2.0**–2.8
RLAMWD mm	0.5–**0.75**–1.1	0.1–**0.68**–2	0.1–**0.7**–2	0.3–**0.6**–1
RACHLN mm	0.65–**1.3**–2	0.5–**1.3**–2	0.5–**1.3**–2	0.8–**1.3**–2
RPAPLN	2.1–**2.9**–3.7	1.3–**2.7**–4.2	1.3–**2.7**–4.2	1.9–**2.4**–3.3
DISCNUM	4–**11.1**–18	3–**9**–24	3–**9.4**–24	8–**11.8**–16
DCORLN	3.5–**4.3**–5.2	2.2–**4.2**–5	2.2–**4.1**–5	2.7–**3.9**–5
DLOBLN	0.5–**0.77**–1	0.2–**0.9**–1.1	0.2–**0.94**–1.3	0.5–**0.9**–1.5
DACHLN	0.85–**1.3**–2	0.5–**1.3**–2.5	0.5–**1.3**–2.5	0.7–**1.3**–2
DPAPLN*	2.1–**3.4**–4.25	2.1–**3.3**–6	2.1–**3.3**–5	2.3–**2.9**–3.7

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